



PROCEEDINGS OF THE  
CALIFORNIA ACADEMY OF SCIENCES

February 15, 1977

Series 4, Volume 41, Number 1, 123 Pages, 45 figures

**THE OSTEOLOGY, CLASSIFICATION, AND RELATIONSHIPS  
OF THE EEL FAMILY OPHICHTHIDAE**

By  
**John E. McCosker**

*Steinhart Aquarium, California Academy of Sciences  
San Francisco, California 94118*

**ABSTRACT.** A classification of the genera of the apodal family Ophichthidae is proposed on the basis of internal and external morphology, with particular emphasis on osteological characters. Specimens of 89 ophichthid species from 44 genera and comparative material from ten other apodal families were prepared for osteological examination, usually by a trypsin-based staining and clearing technique, and critically compared. Forty-nine ophichthid genera are recognized and are distributed among six tribes in two subfamilies. Diagnostic characters for the recognition of genera include the shape and condition of elements of the gill arch and hyoid arch, number and placement of branchiostegal rays along the hyoid, suspensorium elements, neurocrania, dentition, pectoral girdle elements, cephalic pore patterns, lateral line ossification, fin placement, and morphometric characters. The Ophichthidae are defined on the basis of their numerous overlapping branchiostegals, supraorbital canals united by a transverse commissure through the fused frontals, first and second epibranchial interconnections, absence of a palatine, and the separation of the pterygoid from the vomer. A monophyletic origin of the family from a congrid-like ancestor is proposed. An evolutionary history of the Ophichthidae is suggested, in which the subfamily Myrophinae has separated into two tribes and the subfamily Ophichthinae has radiated into four tribes. The validity of the family name Ophichthidae is discussed. The family names Ophisuridae, Myridae, Myrophidae, Muraenichthyidae, Echelidae, Neenchelidae, Aoteidae, Acanthenchelyidae and Sphagebranchidae are synonyms of the name Ophichthidae. A comparison is made between an ophichthid classification based primarily on osteology and the previous classification, based primarily on external morphology. The results of two computer-programmed classification schemes of species relationships within a single tribe are compared with a classification developed using traditional methodology. Alternate hypotheses are proposed to explain the log-normal inverse relationship between genera and the distribution of species among genera in the Ophichthidae.



## TABLE OF CONTENTS

	Page
LIST OF FIGURES .....	5
LIST OF TABLES .....	6
ACKNOWLEDGMENTS .....	7
INTRODUCTION .....	9
General .....	9
History of Ophichthid Classification .....	10
Validity of the Family Name .....	10
Osteological Studies of the Ophichthidae .....	11
Familial Synonymy of the Ophichthidae .....	12
Synopsis of Ophichthid Classification .....	13
METHODS .....	14
Taxonomic Methods .....	14
Abbreviations .....	14
Materials Examined .....	15
Statistical Methods .....	16
OSTEOLOGY AND FUNCTIONAL ANATOMY .....	17
Neurocranium .....	18
Suspensorium and Jaws .....	24
Opercular Series .....	26
Hyoid Apparatus .....	28
Gill Arches .....	32
Pectoral Girdle .....	33
Lateralis System .....	36
Axial Skeleton .....	42
Caudal Skeleton .....	45
Visceral Anatomy .....	48
TAXONOMY .....	48
Osteological Definition of the Ophichthidae .....	49
Analytical Key to the Genera of Ophichthidae .....	50
Kaup's Genera .....	56
Subfamilial and Tribal Diagnoses and Generic Descriptions .....	57
Subfamily Myrophinae .....	57
Tribe Benthenchelyini (Genera are listed alphabetically within each tribe) .....	57
Tribe Myrophini .....	57
Subfamily Ophichthinae .....	62
Tribe Callechelyini .....	62
Tribe Sphagebranchini .....	64
Tribe Bascanichthyini .....	70
Tribe Ophichthini .....	73
Comparison with Previous Classifications .....	85
EVOLUTION OF THE OPHICHTHIDAE .....	85
Relationship to other Anguilliforms .....	85
Evolution within the Ophichthidae .....	86
Myrophini and Benthenchelyini .....	88
Ophichthini .....	89
Sphagebranchini .....	91
Bascanichthyini .....	94
Callechelyini .....	94
ZOOGEOGRAPHY AND COMMENTS ON OPHICHTHID SPECIATION .....	96
LITERATURE CITED .....	101
TABLES .....	108
INDEX TO GENERA AND SPECIES .....	120



## LIST OF FIGURES

Figure	Page
1 An Early Illustration of an Ophichthid, presumably <i>Ophisurus serpens</i> .....	8
2 Neurocranium of <i>Ophichthus zophochir</i> .....	18
3 Neurocranium of <i>Ophichthus zophochir</i> .....	18
4 Neurocranium of <i>Benthenchelys cartieri</i> .....	19
5 Neurocranium of <i>Myrophis vafer</i> .....	19
6 Neurocranium of <i>Muraenichthys chilensis</i> .....	19
7 Neurocranium of <i>Callechelys marmoratus</i> .....	19
8 Neurocranium of <i>Ichthyapus selachops</i> .....	20
9 Neurocranium of <i>Stictorhinus potamius</i> .....	20
10 Neurocranium of <i>Bascanichthys panamensis</i> .....	20
11 Neurocranium of <i>Myrichthys xystrurus</i> .....	20
12 Otoliths of Several Ophichthid Species .....	23
13 Head skeleton of <i>Ophichthus zophochir</i> .....	24
14 Suspensorium and Jaws of <i>Ophichthus zophochir</i> .....	25
15 Right Postorbital Series of <i>Brachysomophis sauropsis</i> .....	26
16 Maxilla-Vomer Apposition of Several Ophichthids .....	27
17 Hyoid Arch and Branchiostegals of <i>Ophichthus zophochir</i> , an Ophichthine, and <i>Muraenichthys chilensis</i> , a Myrophine .....	29
18 Gill Arch Skeleton of <i>Ophichthus zophochir</i> .....	31
19 Pectoral Girdle of Various Representative Ophichthines .....	34
20 Pectoral Girdle of Various Representative Myrophines .....	35
21 Cephalic Lateralis System and Associated Bones .....	37
22 Lateral Line Ossicles of Representative Ophichthines .....	39
23 Lateral Line Ossicles of Representative Myrophines .....	40
24 Cephalic Pore and Surface Sensory Papillae Development in Two Ophichthids ....	41
25 Antermost Five Vertebrae of the Type Genera of the Tribes of Ophichthids ....	43
26 Trunk and Caudal Vertebrae of <i>Ophichthys zophochir</i> .....	44
27 Caudal Skeleton of <i>Ophichthus zophochir</i> .....	46
28 Caudal Skeleton of <i>Myrophis vafer</i> .....	47
29 Comparative Anatomy of Congrid and Ophichthid Digestive Tract and Gas Bladder .....	49
30 Vomer, Maxillae, and Pterygoid of <i>Ahlia egmontis</i> and <i>Myrophis vafer</i> .....	50
31 Diagrammatic Representation of a Species with Well Developed Head Pores .....	51
32 Representation of Underside of Callechelyin Snouts .....	52
33 Diagrammatic Representation of Posterior Trunk Vertebrae .....	52
34 Diagrammatic Representation of Head and Pectoral Fins of Two Ophichthins .....	55
35 Diagrammatic Representation of an Ophichthin with a Fringed Upper Lip .....	56
36 Opercular Series of <i>Myrophis vafer</i> .....	60
37 Proposed Evolutionary Relationships of Ophichthid Tribes .....	86
38 Proposed Evolution of the Myrophinae .....	87
39 Proposed Evolution of the Ophichthini .....	90
40 Proposed Evolution of the Sphagebranchini .....	92
41 Proposed Evolution of the Bascanichthyini .....	93
42 Proposed Evolution of the Callechelyini .....	95
43 Phenogram of the Relationships of the Callechelyini, Using Program WVGM .....	97
44 Interrelationships of Species Groups of the Tribe Callechelyini, as Defined by Program REGROUP .....	98
45 Distribution of Species Among the Genera of the Ophichthidae, Gobiesocidae and Salariaiini .....	100

## LIST OF TABLES

Table	Page
1 Dentition of the Genera of Ophichthidae .....	108
2 Number and Location of Branchiostegal Rays of the Species of the Ophichthidae ....	109
3 Gill Arch Condition in the Ophichthinae .....	110
4 Gill Arch Condition in the Myrophinae .....	111
5 Lateral Line and Cephalic Pore Conditions in Ophichthine Genera and Subgenera ..	112
6 Vertebral Counts of Various Ophichthid Species .....	113
7 Characteristics of the Ophichthidae and Related Eel Families .....	116
8 Morphological and Meristic Characters of the Species of the Callechelyini .....	117
9 Characteristics of the Species of Callechelyini Used in Programs REGROUP and WVGM .....	118
10 Distribution of Certain Ophichthid Genera .....	119

### ACKNOWLEDGMENTS

The majority of this work is from my doctoral dissertation done at the Scripps Institution of Oceanography, University of California, San Diego, under the direction of Richard H. Rosenblatt and Carl L. Hubbs. I sincerely thank Professor Hubbs for his advice and guidance through the capricious nuances of zoological nomenclature, and Professor Rosenblatt for his invaluable advice, encouragement, and patience throughout the duration of my graduate studies.

I wish to express my gratitude to the following individuals who have made various specimens available: Marie-Louise Bauchot, Paris Museum; Jacques Blache, Centre ORSTOM; James E. Böhlke, Academy of Natural Sciences of Philadelphia; Peter H. J. Castle, Victoria University of Wellington, New Zealand; Lev Fishelson, Hebrew University; John E. Fitch, California Department of Fish and Game; Warren C. Frehofer, then of Stanford University; Robert H. Gibbs, Jr. and Robert H. Kanazawa, National Museum of Natural History; William A. Gosline, then of University of Hawaii; Naercio A. Menezes, Universidade de São Paulo; Hans Nijssen, Zoologisch Museum Amsterdam; John R. Paxton and Douglass F. Hoese, Australian Museum; John E. Randall,

Bernice P. Bishop Museum; Tyson R. Roberts, Museum of Comparative Zoology, Harvard University; C. Richard Robins, University of Miami Marine Laboratory; Margaret M. Smith, Rhodes University; Enrico Tortonese, Museo Civico di Storia Naturale, Genova; Boyd W. Walker and John Bleck, University of California, Los Angeles. I am particularly grateful to William N. Eschmeyer and the staff of the California Academy of Sciences for making the extensive and critical material from the George Vanderbilt Collections available to me.

Thanks are also due to the following individuals: Ira Rubinoff and the staff of the Smithsonian Tropical Research Institute for assistance during my tenure as a Smithsonian pre-doctoral research fellow; Edward W. Fager and John H. Wormuth for assistance with computer programs; students and colleagues at Scripps Institution, and in particular Joseph F. Copp and Donald M. Dockins, for aiding in numerous ways; Richard H. Rosenblatt, Carl L. Hubbs, Robert R. Hessler, and Peter Paul Vaughn for their critical reading of my dissertation; and my wife, Sandra, for her help and encouragement.

## SERPENT MARIN.

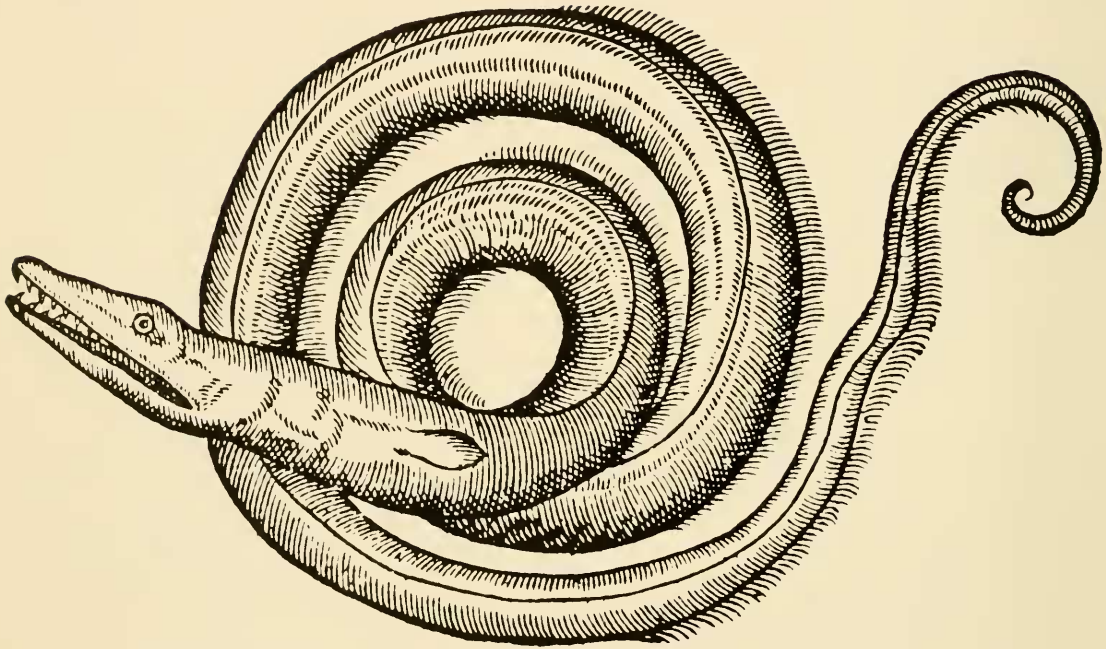


Figure 1. An early illustration of an ophichthid eel, presumably *Ophisurus serpens*, from Mattioli's *Commentaires* (1568).



## THE OSTEOLOGY, CLASSIFICATION, AND RELATIONSHIPS OF THE EEL FAMILY OPHICHTHIDAE

By

John E. McCosker

### INTRODUCTION

#### *General*

The Ophichthidae comprise a large family of mostly fossorial eels limited to continental shelf depths of all tropical and subtropical oceans. The Ophichthidae contains more than 200 species here distributed among 49 genera, representing perhaps the greatest diversity of anatomical specializations within a single apodal family. The resemblance of many ophichthids to snakes has earned them the common name of "snake-eels," and along with the morays, have evoked many sea-serpent legends among tropical coastal peoples. Perhaps the earliest illustration identifiable as an ophichthid (fig. 1) was that of Mattioli (1568) p. 388, probably based on an adult *Ophisurus serpens*. The first described ophichthid species, *Muraena ophis*, was the second apodal fish in Linnaeus' *Systema Naturae* (1758).

The taxonomic treatment of the Ophichthidae, and of apodal fishes in general, has been in constant flux since the eighteenth century, and only within the past two decades has a coherent concept of the Ophichthidae become realized. Previous theories of the interrelationships of ophichthid genera have been based on such trivial characters as fin position, dentition types and coloration. It is now generally accepted that the osteology more conservatively reflects the phylogeny of a group and is less affected than external morphology by minor evolutionary adaptations. The unsatisfactory state of the classification of the ophichthids has been recognized by numerous authors (Myers and Storey, 1939; Myers and Wade, 1941; Gosline, 1951a; Smith, 1964; Rosenblatt and McCosker, 1970; Robins and Robins, 1971; Castle, 1972) most of whom have concluded that an osteological revision of all included genera was necessary for a proper understanding of the family. The aim and scope of this study have been directed to that objective.

### History of Ophichthid Classification

The 218 years since Linnaeus' (1758) description of the first ophichthid species have witnessed a plethora of generic and specific names applied to the Ophichthidae. The first generic name properly applied to an ophichthid was *Ophichthus* (Ahl, 1789), which should more properly have been written "*Ophichthys*". The emendations of Ahl's generic spelling by subsequent authors have resulted in confusion over the generic and familial names. This problem was briefly treated by Gosline (1951a: p. 298) and is further illuminated in the following discussion.

The treatment of apodal taxonomy was in constant flux during the eighteenth and nineteenth centuries, which accounts for much of the lack of uniformity in nomenclature. Swainson's (1838) treatment of the eel-like fishes was based largely on Cuvier's work (1817), and was the first attempt at an arrangement of the eels into family groups. Swainson (p. 215) designated the "*Muraenidae* (as) having two branchial spiracles in their ordinary position, and the *Sphagebranchidae*, or sea eels, where the branchial spiracles are either close together or united into one." Confusion ensues on the following page where the family name Gymnarchidae is apparently considered synonymous with the Symbbranchidae, and further evidenced in his discussion (p. 218) of the gill openings, by his statement that "among the *Gymnarchidae*, or sea eels, for instance, they are close together and united under the throat as in *Sphagebranchus*." Swainson divided the Muraenidae into two subfamilies, the Anguillinae and the Muraeninae, both of which contained species now known to be ophichthids. McClelland (1844) realigned the apodal classifications of Swainson and Cuvier and created the family Ophisuridae to include eels with a rayless caudal containing the genera *Leptognathus* (= *Ophisurus*), *Ophisurus*, and *Ophithorax* (= *Ophichthus*). Kaup (1856a,b) disregarded most of McClelland's classification without comment, but did retain the name Ophisuridae. Kaup divided the apodal fishes into two "sections". These were the Cryptomycteres (containing only the Ophisuridae) which included those eels with labial nostrils, and the Phaneromycteres which contained all other apodal families. The ophisurids were divided into three subfamilies, the Ophisurinae, the Sphagebranchinae, and the Myrophinae (containing *Myrus*, *Myrophis*, and *Muraenichthys*). Bleeker, in his *Systema Muraenorum Revisum* (1865), recognized the family Ophisuroidei and considered

the Myrophinae (as Myriformes) to be a subfamily of the family Congroidei. Günther (1870) considerably revised previous classification by placing the majority of the known eels into a single family, the Muraenidae, which he divided into ten "Groups". The Ophisuridae of earlier authors was divided into two groups, the Ophichthyina containing those species with a rayless caudal [comprising the genera *Liuranus* (*sic*) with a single species and *Ophichthus* with at least 78 species], and the Myrina containing those with a rayed caudal (comprising *Myrus*, *Myrophis*, *Paramyrus*, *Chilorhinus*, and *Muraenichthys*). Günther's groups were elevated to family rank by Jordan and Davis (1891). The Myrinae became the family Echelidae (Jordan and Davis considered *Myrus* a synonym of *Echelus*) and the Ophichthyina of Günther (actually, the Ophisuroidei of Bleeker) became the Ophisuridae. Uncertainty concerning the synonymy of *Myrus* and *Echelus* resulted in the changing of the name Echelidae to Myridae by Jordan and Evermann (1896) and by Jordan and Snyder (1901). The family name Ophichthyidae, derived from Günther's Ophichthyina, first appeared in Jordan and Evermann (1896). The authors rejected the name Ophisuridae and considered *Ophisurus* a synonym of *Ophichthus*.

### Validity of the Family Name

Confusion relating to the spelling of the Ophichthyidae with a "y" relates to the correction by earlier authors of Ahl's (1789) spelling of *Ophichthus*. The generic name is from the Greek ὄφις, meaning snake, and ἰχθύς, meaning fish, and would more correctly have been written *Ophichthys*. Bleeker, Günther, and other classicists emended Ahl's generic spelling (see Jordan and Gilbert, 1882), but Jordan and his later co-authors returned to Ahl's original spelling. The retention of the original spelling of the generic name but the usage of the emended family name is illogical, and according to the International Code of Zoological Nomenclature, incorrect, as Gosline (1951a) has pointed out. Most recent authors, with few exceptions, have used "Ophichthidae" and "Ophichthys".

A serious difficulty however exists, concerning the earlier family names proposed by Swainson and by McClelland. The inconsistencies in Swainson's usage of Sphagebranchidae would invalidate it as a family name. Although *Sphagebranchus* Bloch (1795) was then a valid genus and properly an ophichthid, *Gymnarchus*, a gymnarchid, was

later shown not to be an apodal fish. The problem of recognizing McClelland's usage of *Ophisuridae* was avoided by Gosline who stated that "whether or not *Ophisurus* is a valid genus is a moot nomenclatorial question. Consequently I prefer not to use for this family, at the present time, the little-known and possibly invalid name *Ophisuridae*." The logical solution to this nomenclatorial dilemma seems to be the invoking of the plenary powers of the International Commission on Zoological Nomenclature. The suppression of the rarely used name *Ophisuridae* in favor of the universally recognized name *Ophichthidae* would clearly be in the interests of stability.

#### *Osteological Studies of the Ophichthidae*

Regan (1912) was the first to attempt an osteological definition of the *Ophichthidae*. Most importantly, his emphasis on the fused frontals of the ophichthids, congrid, and relatives has remained as a fundamental character in our concept of eel evolution. The other osteological characters identified by Regan ("caudal vertebrae with transverse processes" and "maxillaries articulating with ethmoid near the end of the snout") only described certain members of the family. His separation of the congrid from the ophichthids, on the basis of their long and slender rather than vestigial neural spines, was also an important observation. Trewavas' (1932) apodal classification scheme followed Regan's characterization of the ophichthids. For nearly two decades, subsequent ophichthid studies dealt only with superficial characters. An exception was that of Myers and Storey (1939) who noticed the overlapping of the branchiostegal rays in ophichthid species. They pointed out that these rays are similar to the "jugostegalia" described by Parr (1930) in echelid eels. On that basis, and other external morphological similarities, Myers and Storey suggested that the *Echelidae* might be merged with the *Ophichthidae*.

Gosline (1950, 1951a, 1951b, 1952), in a series of papers, analyzed the species referred to the *Echelidae* and the *Ophichthidae*. His osteological study of *Kaupichthys diodontus* (1950) demonstrated that its osteology precluded its inclusion in the same family with *Muraenichthys cookei*. He found (p. 312-314) that *K. diodontus* differs in having sutured frontals and non-overlapping branchiostegal rays, as well as several other characters which later proved to be non-definitive. Lacking a specimen of *Echelus myrus*, Gosline was unable to further define the *Echelidae*, but suggested that species of *Myrophis* and *Muraen-*

*ichthys* might be referred to the *Ophichthidae*, to comprise the subfamily *Myrophinae*, on the basis of their "basket-like arrangement of the numerous, long branchiostegal rays." In a following paper, Gosline (1951b) described the osteology of *Chilorhinus brocki* (= *C. platyrhynchus*) and related it to *Kaupichthys diodontus*. He suggested that the external similarities of species of *Kaupichthys*, *Chilorhinus* and ophichthids are "the result of parallel evolution and not of close genetic relationship." His prediction that *Echelus*, once examined on an osteological basis, would prove to be confamilial with *Kaupichthys* was incorrect (Gosline, 1952; Böhlke, 1956a).

Gosline (1951a), in a more comprehensive paper, prepared the first diagnostic treatment of the *Ophichthidae*. His study, however, was limited to those species occurring in the Hawaiian area and thus did not include several critical genera. He compared the *Ophichthidae* with the *Congridae* (primarily *Conger*), and concluded that the ophichthid conditions are derived from, and more advanced than, those of their more primitive congrid ancestors. Two subfamilies within the *Ophichthidae* were recognized (the *Myrophinae* and the *Ophichthinae*) although osteological differences other than the caudal skeleton were not defined. In a subsequent paper, Gosline (1952) described the morphology of *Echelus myrus* in detail and concluded that it was referable to the ophichthid subfamily which contained *Myrophis* and *Muraenichthys*. On that basis he changed the subfamilial name of the *Myrophinae* to *Echelinae*. The results of that study did not alter his earlier (1951a) diagnosis of the family.

Subsequent studies dealing with ophichthid osteology followed Gosline's (1951a) general definition of the family, but amended his diagnosis to include genera that he had not examined. Böhlke (1960) added *Pseudomyrophis*, and provisionally *Neenchelys*, to the *Ophichthidae*. In doing so, he expanded the familial diagnosis to allow the following: posterior nostrils either lateral or labial; maxillary articulation variable in position along the ethmoid; pharyngeal openings of the branchial clefts may be reduced; transverse processes of the caudal vertebrae either present or absent.

Nelson's (1966a) analysis of apodal gill arch conditions found most ophichthids to be "distinguished in having the proximal ends of the dorsal parts of the first and second arches connected through a continuous cartilage, a peculiarity not present in any other of the eel families studied." Certain generic lineages were identified

on the basis of their gill arch configurations. Nelson's (1966b) study of the osteology of *Neeenchelys buitendijki* confirmed Böhlke's earlier supposition of its placement within the Ophichthidae. Nelson separated the ophichthids from the congrid in the following manner: posterior nostril usually opening on the ventral surface of the upper lip; tongue adnate; branchiostegal rays overlapping along the midventral line; supraorbital canals united by the transverse frontal commissure; neural spines absent. Castle's (1972) osteological study of *Benthenchelys cartieri* summarized the diagnoses from Gosline's, Böhlke's, and Nelson's earlier works, but did not contribute to or amend their diagnoses.

#### *Familial Synonymy of the Ophichthidae*

The Ophichthidae, as currently recognized, includes several families which were until recently considered distinct. The basis and validity of studies resulting in these actions are discussed below.

The family Neenchelidae was erected by Bamber (1915) to contain *Neeenchelys microtretus*, a new genus and species from the Red Sea. It was considered to be closely related to the Muraenesocidae as defined by Regan (1912). A second neenchelid, *N. buitendijki*, was described by Weber and de Beaufort (1916) from the Indo-Australian archipelago. The family received no further definitive treatment until Böhlke (1960), on the basis of Bamber's description, suggested that *Neeenchelys* may be related to species of *Pseudomyrophis* and thus properly be considered an ophichthid of the subfamily Echelinae (sensu Gosline, 1951a, 1952). The collection of adequate material of *N. buitendijki* and its osteological examination by Nelson (1966b) supported Böhlke's prediction. Nelson's (1967) examination of the holotype of *N. microtretus* confirmed the recognition of the Neenchelidae as ophichthids in the subfamily Echelinae (herein considered as Myrophinae).

The Acanthenchelyidae also belongs in the Ophichthidae. Family recognition was short-lived, consisting of Jordan, Evermann, and Clark's (1930) elevation of *Acanthenchelys* Norman (erroneously attributed to Regan) to family status, but this was largely ignored by later authors. Randall and Robins (1966) relegated *Acanthenchelys* to the synonymy of *Ophichthus*, an action which is followed here.

The Aoteidae are provisionally included in the Ophichthidae. The Aoteidae were first recognized

as ophichthids by Castle (1967), who referred the single aoteid species to the genus *Muraenichthys*.

The family Echelidae (=Myridae, Myrophinae, Myrophidae, and Muraenichthyidae), has been a catch-all group with a checkered history. The echelids were considered congrid or muraenesocid relatives by most nineteenth century authors. Bleeker (1865), for example, considered the Myriformes (containing *Myrophis*, *Echelys*, and *Muraenichthys*) to be a subfamily of the Congroidei. Kaup (1856a, b) was exceptional in placing considerable importance on the labial nostril condition, and in allying the Myrophinae with the Ophisurinae as a single unit which excluded the congroids and relatives. Twentieth century authors considerably expanded the Myrophidae (which was to become known as the Echelidae, fide Jordan and Evermann, 1896) to include as many as 22 genera at various times (Schultz and Woods, 1949). The dissection of this large and cumbersome family was initiated by Myers and Storey (1939), and was followed by Schultz and Woods (1949) and by Gosline (1950, 1951a, b, 1952). Myers and Storey noted the presence of accessory branchiostegal rays (the "jugostegalia" of Parr, 1930) in both ophichthids and echelids, but were hesitant to merge the families without an extensive anatomical examination. Gosline (1951a) established the similarities of the two families on an osteological basis and included the genera *Myrophis* and *Muraenichthys* in the Ophichthidae to comprise the subfamily Myrophinae. His subsequent (1952) osteological examination of *Echelus myrus* resulted in its inclusion into the family, and the replacement of the name Myrophinae with Echelinae. The present study has demonstrated that Gosline was correct in considering the Myrophines to be ophichthids, but erred in including *Echelus* with the Myrophinae. Although certain authors have continued to recognize a family Echelidae for the forms with caudal rays (e.g., J. L. B. Smith, 1962; Blache, 1968), no convincing arguments have been proposed which would merit familial separation. Blache's (1968: 1501) continued usage of the name Echelidae, with the justification that "... nous sommes également, tout à fait, partisan de cette position et nous ne conservons ici, la famille des Echelidae, que pour des raisons artificielles de commodité taxonomique," is both illogical and incorrect.

Further substantiation of the inclusion of the Echelidae with the Ophichthidae is evidenced in the leptocephalus larval stage. (The leptocephalus of *Neeenchelys* has not been identified.)

Eel leptocephali display evolutionarily conservative features that could prove useful in phylogenetic investigations (Castle, 1965, 1967), yet the problem of generic and specific identification still remains and has precluded their usage in this study. It is important to note, however, that the morphology of ophichthid leptocephali reflects the family grouping fairly well. Castle (1965) and D. Smith (unpub. MS) have diagnosed the ophichthid leptocephalus as moderately elongate when full grown, characteristically possessing gut thickenings or loops which usually accompany swellings of the pronephric ducts, conspicuously pigmented with patches of chromatophores which occasionally occur on the head, at various points along the gut, and often on the myosepta, lateral caudal midline, and dorsal and anal bases, and possessing a moderate to blunt tail. Castle (1965: 98) has stated that "the pectoral remains obvious throughout larval life, probably even in those ophichthids which show loss of the pectoral in the juvenile and adult." Phylogenetic implications at the generic level would therefore be further evidenced in this conservative larval condition if Castle's suggestion proves correct. For example, his tentative identification of *Leptocephalus Muraenichthys* sp. is based on a leptocephalus possessing a short, rounded pectoral fin (Castle, 1965: figs. 2F, G), not unlike that of *Myrophis* (Eldred, 1966; Castle, 1965: figs. 3e-f).

In contrast to the above mentioned families, the *Macrocephenchelyidae* was incorrectly synonymized with the *Ophichthidae*. This family, known only from the holotype and damaged paratype of *Macrocephenchelys brachialis* Fowler, was synonymized without comment with the *Ophichthidae* by McAllister (1968: 85). Robins and Robins (1971) have re-erected the family on the basis of a thorough osteological examination of the paratype. They have shown its affinities to be with the *Congridae* and referred it to the superfamily *Congroidea*. *Macrocephenchelys* displays several characters quite divergent from the *Ophichthidae*, including the extensive ossification of the branchial apparatus (yet there is no lower pharyngeal tooth plate), the absence of the transverse frontal commissure of the cephalic lateralis system, and the presence of eight stout branchiostegal rays and a complete palatopterygoid arch.

*Synopsis of Ophichthid Classification*

The listing of nominal taxa below summarizes the taxonomic conclusions of this study. Full descriptions of new taxa and complete generic synonymies are presented later in this paper.

Subfamily Myrophinae

Tribe Benthenchelyini

*Benthenchelys* Fowler 1934

Tribe Myrophini

*Ahlia* Jordan and Davis 1891

*Muraenichthys* Bleeker 1853

Subgenus *Muraenichthys* Bleeker 1853

Subgenus *Scolecenchelys* Ogilby 1897

*Myrophis* Lütken 1851

*Neenchelys* Bamber 1915

*Pseudomyrophis* Wade 1946

*Schismorhynchus* McCosker 1970

*Schultzidia* Gosline 1951

Subfamily Ophichthinae

Tribe Callechelyini

*Aprognathodon* Böhlke 1966

*Callechelys* Kaup 1856

*Letharchus* Goode and Bean 1882

*Leuropharus* Rosenblatt and McCosker 1970

*Paraletarchus* McCosker 1974

Tribe Sphagebranchini

*Achirophichthys* Bleeker 1865

*Apterichthys* Duméril 1806

*Caecula* Vahl 1794

*Cirraecacula* Schultz 1953

*Hemerorhinus* Weber and de Beaufort

1916, *incertae sedis*

*Ichthyapus* de Barneville 1847

*Lamnostoma* Kaup 1856

*Stictorhinus* Böhlke and McCosker 1975

*Yirrkala* Whitley 1940

Tribe Bascanichthyini

*Allips* McCosker 1972

*Bascanichthys* Jordan and Davis 1891

*Caralophia* Böhlke 1955

*Dalophis* Rafinesque 1810

*Etheadophis* Rosenblatt and McCosker 1970

*Gordiichthys* Jordan and Davis 1891

*Leptenchelys* Myers and Wade 1941

*Phaenomonas* Myers and Wade 1941

Tribe Ophichthini

*Aplatophis* Böhlke 1956

*Brachysomophis* Kaup 1856

*Cirrhimuraena* Kaup 1856

Subgenus *Cirrhimuraena* Kaup 1856

Subgenus *Jenkinsiella* Jordan and

Evermann 1905

*Echelus* Rafinesque 1810

*Echiophis* Kaup 1856

*Elapsopsis* Kaup 1856

*Evips* McCosker 1972

*Leiuranus* Bleeker 1853

*Malvoliophis* Whitley 1934  
*Myrichthys* Girard 1859  
*Mystriophis* Kaup 1856  
*Ophichthus* Ahl 1789  
    Subgenus *Ophichthus* Ahl 1789  
    Subgenus *Microdonophis* Kaup 1856  
    Subgenus *Centrurrophis* Kaup 1856  
    Subgenus *Coecilophis* Kaup 1856  
*Ophisurus* Lacépède 1800  
*Phyllophichthus* Gosline 1951  
*Pisodonophis* Kaup 1856  
*Pogonophis* Myers and Wade 1941  
*Quassiremus* Jordan and Davis 1891  
*Scyalichthys* Jordan and Davis 1891  
*Xyrias* Jordan and Snyder 1901

## METHODS

### Taxonomic Methods

Osteological examinations, whenever possible, were based on entire stained and cleared specimens. Rare specimens and holotypes were studied by gill arch removal and radiographic examination. Radiographs were prepared using a General Electric 40 KV x-ray unit and Kodak Industrial Type M film. Radiographs were either examined under a dissecting microscope or from photographic enlargements. Stained and cleared gill arches or entire specimens were prepared using the trypsin-preparation method of Taylor (1967) and, in certain instances, the modifications of Miller and Landingham (1969). Neurocrania were prepared by dissection, soaking in a 5-7 percent potassium hydroxide (KOH) solution to remove the flesh, and staining in an alizirin bath. Sutures along the dry skulls became more apparent during examination when painted with pure glycerin using a fine camel's hair paint brush. Certain skulls were disarticulated in a 7-10 percent KOH solution to better identify certain sutures. Drawings were made using a camera lucida attachment on a Wild dissecting microscope.

Gill arch terminology is that of Nelson (1969). Bone terminology follows that of Asano (1962) with certain modifications that are identified in the section dealing with bone complexes.

The following measurements, used in the generic key and descriptions, are defined as follows:

*Head length.* Measured from the snout tip to the posterodorsal point of the gill opening.

*Trunk length.* Measured from the posterodorsal point of the gill opening to mid-anus.

*Tail length.* Measured from mid-anus to the tail tip.

*Inclination of the suspensorium.* The suspensorium is considered to be "anteriorly inclined" if the angle formed by the midlines of the hyomandibular and the mandible (when the mouth is closed) is greater than 90°. If the angle is less than 90° the suspensorium is considered to be "posteriorly inclined". This measurement is somewhat subjective, and made either from radiographs or observations of stained and cleared specimens under the dissecting microscope.

All fish lengths are listed as total lengths. Generic descriptions and diagnoses were based on adults unless otherwise stated.

## ABBREVIATIONS

### Anatomical Abbreviations

**A** - anus; **an** - anterior nostril; **AR** - anal fin ray; **B<sub>1</sub>** - first basibranchial; **BO** - basioccipital; **BR** - branchiostegal ray; **BS** - basisphenoid; **C<sub>1</sub>** - first ceratobranchial; **CE** - centrum; **CH** - ceratohyal; **Cl** - cleithrum; **Co** - coracoid; **CTP** - transverse processes of caudal vertebrae; **CX** - cartilaginous extension of terminal vertebra; **D** - dentary; **DFO** - dorsal fin origin; **DR** - dorsal fin ray; **E** - eyeball; **E<sub>1</sub>** - first epibranchial; **EH** - epihyal; **EN** - epineural; **EO** - epiotic; **ET** - ethmoid portion of premaxilloethmovomer; **EX** - exoccipital; **F** - frontal; **GB** - gas bladder; **GH** - glossohyal; **GO** - gill opening; **H** - heart; **H<sub>1</sub>** - first hypobranchial; **HA** - haemal arch; **HH** - hypohyal; **HY** - hypural; **HYM** - hyomandibular; **I** - intestine; **I<sub>2</sub>** - second infrapharyngobranchial; **IM** - intramuscular bone; **io** - infraorbital pore; **IO** - interopercle; **L/D** - relation of length to depth; **LL** - lateral line; **LP** - lower pharyngeal tooth plate; **MX** - maxilla; **N** - nasal; **NA** - neural arch; **NS** - neural spine; **OP** - opercle; **OR** - orbit; **P** - parapophysis; **PA** - parietal; **PAS** - parasphenoid; **PD** - pneumatic duct; **PG** - pterygoid; **PL** - pleural rib; **pm** - preoperculomandibular pore; **PO** - preopercle; **pop** - preopercular pore; **por** - postorbital pore; **POR** - postorbital; **PR** - pectoral fin rays; **Pt** - pterygiophore; **PT** - pterotic; **PTS** - pterosphenoid; **Q** - quadrate; **S** - stomach; **SA** - sagitta; **Sc** - scapula; **SCI** - supra-cleithrum; **so** - supraorbital pore; **SO** - supraoccipital; **SOC** - supraoccipital crest; **SOP** - subopercle; **sp** - surface sensory papillae; **SP** - sphenotic; **stp** - supratemporal pore; **tp** - temporal pore; **UH** - urohyal; **UP** - upper pharyngeal tooth plate; **V** - vertebra; **VO** - vomer.

### Distributional Abbreviations

**EA** - eastern Atlantic; **EP** - eastern Pacific; **IP** - central and Indo-west Pacific; **M** - Mediterranean; **WA** - western Atlantic.

*Institutional Abbreviations*

The following abbreviations are used in reference to material examined:

**ANSP** - Academy of Natural Sciences of Philadelphia; **BPBM** - Bernice P. Bishop Museum; **CAS** - California Academy of Sciences; **DANA** - Carlsbergfondets DANA-Ekspeditioner, Marinbiologisk Laboratorium Charlottenlund Slot, Denmark; **IA** - Australian Museum at Sydney; **LACM** - Los Angeles County Museum; **MCZ** - Museum of Comparative Zoology, Harvard University; **MNHN** - Muséum National d'Histoire Naturelle, Paris; **MSNG** - Museo Civico di Storia Naturale, Genoa, Italy; **MZUSP** - Museu de Zoologia, Universidade de Sao Paulo, Sao Paulo, Brazil; **RU** - Rhodes University, Grahamstown, South Africa; **SIO** - Scripps Institution of Oceanography; **SU** - Stanford University, also listed as **SNHM** for Stanford Natural History Museum, specimens now deposited at the CAS; **TABL** - Southeast Fisheries Center, Miami, Florida; **UCLA** - Fish Collection, Department of Zoology, University of California at Los Angeles; **UMML** - Rosenstiel School of Marine and Atmospheric Science of the University of Miami; **USNM** - National Museum of Natural History, Smithsonian Institution, Washington, D.C.; **ZMA** - Zoologisch Museum Amsterdam.

*Material Examined*

Listed below is the material utilized for osteological examination in this study. The specimens are grouped by tribes and listed alphabetically within each tribe. Following each specific name is the museum abbreviation, museum catalogue number, number of specimens, range of the total length(s) of the specimen(s) involved. Abbreviations are: CS, stained and cleared by the Taylor (1967) trypsin technique; GA, gill arches removed, stained and cleared; H, hyoid removed; S, skull preparation; X, radiograph. Specimens utilized only for vertebral counts are not included in this listing.

Ophichthidae - Benthenchelyini. *Benthenchelys cartieri*, DANA 3735, 2(105-115mm), CS.

Ophichthidae - Myrophini. *Ahlia egmontis*, SIO 67-87, 1(268), S; SIO 71-266, 1(337), CS. *Muraenichthys chilensis*, SIO 65-645, paratype, 1(248), CS; SIO 65-655, paratype, 1(276), CS, 1(292), S. *Muraenichthys gymnopterus*, SIO 69-276, 1(129), S, 1(144), CS. *Muraenichthys gymnotus*, SIO 69-266, 1(244), CS. *Muraenichthys macropterus*, SIO 69-277, 1(181), CS. *Myrophis plumbeus*, SIO 69-

371, 1(182), CS. *Myrophis uropterus*, CAS 13971, 1(159), CS; BPBM 27209, 1(182), CS. *Myrophis vafer*, SIO 68-242, 1(193), CS, 2(265-325), S. *Pseudomyrophis micropinna*, SIO 60-72, 1, head and trunk only, CS. *Pseudomyrophis nimius*, ANSP 110150, 1(350), CS. *Schismorhynchus labialis*, CAS 24687, 5(114-137), CS. *Schultzidia johnstonensis*, SIO 69-267, 1(138), CS.

Ophichthidae - Callechelyini. *Aprognathodon platyventris*, SIO 68-393, paratypes, 2(312-330), CS. *Callechelys bilinearis*, SIO 70-376, 1(260+), CS. *Callechelys cliffi*, SIO 61-247, 1(218), GA, H, X; SIO 65-281, 1(298), GA, H, X. *Callechelys eristigmus*, SIO 65-185, paratype, 1(552), GA, H, X; SIO 65-354, paratype, 1(431), CS. *Callechelys galapagensis*, UCLA 64-40, paratype, 1(767), GA, H, X. *Callechelys holochromus* (holotype of *Cryptopterygium holochroma*), USNM 154994, 1(801), X. *Callechelys luteus*, SIO 68-497, 1(1038), H, X. *Callechelys marmoratus*, SIO 69-269, 1(286), CS, 1(340), S. *Callechelys melanotaenius*, SIO 69-269, 1(401), CS. *Callechelys muraena*, TABL Oregon 2819, 1(235), GA, H, X. *Callechelys nebulosus*, SIO 71-197, 1(283), CS. *Callechelys springeri* (holotype of *Gordiichthys springeri*), USNM 121604, 1(372), X. *Callechelys striatus* SIO 71-165, 1(430), H, X. *Letharchus velifer*, holotype, USNM 31458, 1(396), X. *Letharchus rosenblatti*, SIO 67-40, paratype, 1(248), CS. *Leuropharus lasiops*, holotype, SU 57313, 1(174), GA, X. *Paraetharchus opercularis*, UCLA 64-38, 1(435), GA, X. *Paraetharchus pacificus*, SIO 65-321, 2(276-369), CS.

Ophichthidae - Bascanichthyini. *Allips concolor*, holotype, CAS 13967, 1(375), GA, X. *Bascanichthys panamensis*, SIO 71-98, 1(425), CS; SIO 71-224, 1(295), CS, 1(510), S. *Caralophia loxochila*, SIO 70-228, 1(445), CS; SIO 70-376, 1(238), CS. *Dalophis imberbis*, SIO 72-290, 1(440), GA, X. *Ethadophis byrnei*, holotype, SIO 67-31, 1(508), GA, X. *Ethadophis merenda*, holotype, SIO 65-47, 1(530), GA, X. *Leptenchelys vermiformis*, holotype, USNM 101785, 1(115), X. *Phaenomonas cooperae*, CAS 13964, 2(451-549), CS. *Phaenomonas pinnata* SIO 65-348, 1(375), CS, 1(375), S.

Ophichthidae - Sphagebranchini. *Apterichtus caecus*, MSNG 41058, 1(435), X. *Apterichtus ilavicaudus*, SIO 69-364, 1(300), CS. *Caecula pterygera*, USNM 206375, 1(232), CS. *Cirriacaecula johnsoni*, paratype, USNM 141189, 1(325), CS. *Ichthyapus ophioneus*, SIO 70-376, 1(337), GA, X. *Ichthyapus selachops*, SIO 61-232, 1(400), CS, 1(400), S; SIO 65-343, 1(234), CS. *Ichthyapus vulturis*, holotype, ZMA 104.153, 1(240), X; SIO 69-

366, 1(446), GA, X. *Lamnostoma kampeni*, SU 24593, 1(435), GA, X. *Lamnostoma orientalis*, CAS 13959, 1(205), CS; CAS 13968, 1(229), CS. *Stictorhinus potamius*, MZUSP 8959, paratype, 1(289), CS. *Yirrkala kaupi*, SU 26827, 1(345), GA, X. *Yirrkala lumbricoides*, CAS 13969, 1(346), CS; paratype of *Y. chaselingi*, IA 16190-601, 1(560), X. *Yirrkala misolensis*, CAS 13965, 1(335), CS. *Yirrkala tenuis*, SIO 71-165, 1(370), CS. *Yirrkala* sp., BPBM 11858, 1(306), CS.

Ophichthidae - Ophichthini. *Aplatophis chauliodus*, UMML 27209, 1(165), CS. *Brachysomophis sauropsis*, SIO 69-267, 1(323), CS; SIO 69-271, 1(197), CS. *Cirrhimuraena macgregori*, SIO 68-434, 2(291-317), CS. *Cirrhimuraena taeniopterus*, CAS 13962, 1(445), GA, H, X. *Elapsopsis cyclorhinus*, SIO 69-267, 1(268), CS, 1(475), GA. *Echelus myrus*, SIO 69-369, 1(449), dissected. *Echelus pachyrhynchus*, SIO 69-370, 1(355), CS. *Echiopsis* sp., UMML 29144, 1(298), CS. *Evips percinctus*, holotype, CAS 13966, 1(125.5), GA, X. *Leiuranus semicinctus*, SIO 61-132, 1(195), CS; SIO 69-268, 1(243), CS; SIO 69-273, 1(344), S. *Malvoliophis pinguis*, IA 3646, 1(470), CS. *Myrichthys colubrinus*, SIO 69-272, 1(345), CS. *Myrichthys maculosus*, SIO 68-497, 1(390), CS; SIO 69-272, 1(310), CS. *Myrichthys xystrurus*, SIO 65-335, 1(420), S; SIO 65-354, 2(243-268), CS. *Myrichthys* sp., SIO 34-371, 1(386), CS. *Ophichthus altipinnis*, CAS 14647, 1(915), GA, X. *Ophichthus cephalazona*, SIO 69-279, 2(230-330), CS. *Ophichthus erabo*, CAS 13960, 1(480), GA, H, X. *Ophichthus ophis*, SU 51724, dissected. *Ophichthus rutidodermatoides*, CAS 28727, 1(330), CS. *Ophichthus triserialis*, SIO 61-193, 1(230), CS; SIO 69-252, 1(800), S, prepared skeleton. *Ophichthus zophochir*, SIO 60-304, 1(217), CS; SIO 65-166, 1(310), S, 1(340), S. *Ophisurus serpens*, RU 76-78, 1(325), CS. *Phyllophichthus xenodontus*, SIO 69-273, 2(270-305), CS. *Pisodonophis boro*, SIO 69-281, 1(410), CS. *Pisodonophis cancrivorus*, SIO 69-307, 1(345), CS. *Pisodonophis cruentifer*, MCZ 34529, 1(235), CS. *Pisodonophis daspilotus*, SIO 72-73, 1(251), CS. *Pogonophis fossatus*, SIO 61-227, 2(232-249), CS. *Quassiremus evionthas*, UCLA 64-19, 1(283), GA, X. *Quassiremus nothochir*, SIO 65-334, 2(271-342), CS. *Scyalichthys miurus*, CAS 13970, 1(235), CS. *Xyrias revulsus*, holotype, SU 6476, 1(890), GA, X.

Comparative Material - Non-ophichthids. The following material was stained and cleared with two exceptions. These, *Gymnothorax mordax* and *Muraenesox coniceps*, were examined from prepared skeletons.

Anguillidae. *Anguilla rostrata*, SIO 69-254, 1(210).

Muraenidae. *Anarchias galapagensis*, SIO 65-345, 1(130). *Echidna nebulosa*, SIO 59-8, 1(178). *Enchelycore bayeri*, CAS GVF 1957-18, 1(255). *Gymnothorax castaneus*, SIO 65-291, 1(140). *Gymnothorax mordax*, SIO skeletal collection, 1(ca. 1 meter). *Gymnothorax panamensis*, SIO 61-239, 1(180). *Gymnothorax schismatorhynchus*, CAS GVF 1958-13, 1(265). *Muraena lentiginosa*, SIO 65-354, 1(165). *Uropterygius necturus*, SIO 65-302, 1(175).

Simenchelyidae. *Simenchelys parasiticus*, SIO 68-479, 1(295).

Derichthyidae. *Derichthys serpentinus*, SIO 60-239, 1(140).

Serrivomeridae. *Serrivomer sector*, SIO 63-374, 1(305).

Nemichthyidae. *Nemichthys scolopaceous*, SIO 65-243, 1(440).

Heterenchelyidae. *Pythonichthys asodes*, paratype, UMML 23481, 1(290).

Muraenesocidae. *Muraenesox coniceps*, SIO skeletal collection, a large adult.

Moringuidae. *Moringua ferruginea*, SIO 68-531, 1(305).

Congridae. *Ariosoma gilberti*, SIO 62-709, 3(175-190). *Conger cinereus*, SIO 68-531, 1(210). *Gorgasia punctata*, SIO 62-270, 1(365). *Taenioconger* sp., SIO 62-42, 1(235).

Xenocoelidae. *Chlopsis apterus*, LACM 32555, 2(152-155). *Kaupichthys hyoproroides*, SIO 67-45, 2(150-190).

#### Statistical Methods

Comparisons of vertebral means and variances were made with a standard "t" test. Two computer-programmed grouping techniques were used to compare inter- and intra-generic relationships within the Callechelyini. These were modifications of a clustering technique, the weighted variable group method (WVGM) of Sokal and Michener (1958), and of a recurrent group analysis (REGROUP) devised by Fager (1957). Each will be discussed briefly, although the original sources should be referred to if further information is desired.

Wormuth's (1971) modification of WVGM, used by him in ommastrephid squid taxonomy, was used to identify the interspecific relationships of 18 of the 21 species of the Callechelyini. Cluster analysis is a technique widely used by numerical taxonomists, wherein each species (or individual) is termed an operational taxonomic



unit (OTU). The program, as described by Wornuth (1971), operates in the following manner:

Initially a matrix of  $m$  characters by  $n$  OTU's is set up and the values in each row are standardized using row means and variances. From the standardized matrix ( $m \times n$ ) a product moment correlation coefficient is calculated. This matrix expresses the relationships between all possible pairs of OTU's quantitatively. At this point a clustering procedure is employed to extract a graphic representation of the information contained in the correlation matrix. Any pair of OTU's which has a higher correlation with each other than either has for any other OTU is put together as a group. An average correlation coefficient is computed for each group and it is, thenceforth, treated as a single OTU. In the WVGM a variable number of new groups are formed on each cycle. At the end of each cycle, correlation coefficients are recomputed based on the previous matrix. On any single clustering cycle two alternatives are available. One permits only groups of two OTU's to form prior to recomputation of the correlation matrix if their incorporation lowers the overall group correlation value by less than a preselected amount. As the results of both alternatives over a number of trials were very similar, the latter option was selected for its shorter computation time. The levels at which groups are formed are plotted. The graphical representation of the results is termed a phenogram.

Data and characteristics used in program WVGM for the Callechelyini are presented in tables 8 and 9.

Recurrent group analysis was devised by Fager (1957) to identify communities of species on the basis of their co-occurrence in samples (Fager and McGowan, 1963; Fager and Longhurst, 1968) and later modified for taxonomic purposes by Ebeling and Weed (1963) and by Fager (1969). For each species pair, the program calculates an index of affinity. Fager and McGowan (1963) state that this index does not follow the hypergeometric distribution exactly, and have therefore replaced it with the geometric means of the proportion of common characteristics, corrected for the number of characteristics recorded for the species, such that:

$$I = \frac{J}{\sqrt{A \times B}} - 1/2 \sqrt{B}$$

where  $I$  = index of affinity,  $J$  = number of common characteristics,  $A$  and  $B$  = total characteristics recorded for species  $A$  and species  $B$ , and

where  $B = A$ . All characteristics are equally weighted. From the matrix of species pairs which is generated the largest possible group of species is selected. A "breakpoint" is selected such that pairs of species in which  $I$  is greater than or equal to that point are considered to show affinity. For example, the selection of 0.500 as a breakpoint would group species which share somewhat more than "half" their characteristics. In this study, breakpoints of 0.500 and 0.600 were utilized, the latter appearing to give more reasonable groups without involving excessive alternative and unnatural groups. Once selected, the largest group is removed and the procedure is continued until all possible groups are formed. Where two or more groups of equal size are possible, the program selects the one for which the sum of species pairs' affinity indices is largest. Intergroup relationship can be calculated using the sum of characteristics shared by members of each group as a fraction of the total possible connections (see fig. 44). Inter-group similarity is therefore directly related to this fraction.

It should be noted that the computer programs used are each affected by the amount of, and manner in which, data are presented. The sensitivity of each program increases with increased data input. REGROUP is particularly insensitive to continuous data (e.g., vertebral and branchiostegal ray numbers, body proportions) and treats each data interval equally. WVGM, by contrast, takes account of continuous data in calculating a correlation coefficient, but is somewhat more insensitive to dichotomous and trichotomous data. The characteristics used in each program are identified in tables 8 and 9.

## OSTEOLOGY AND FUNCTIONAL ANATOMY

In the following section the osteology of *Ophichthus zophochir* is described and illustrated in detail. The bone complexes are treated separately, each beginning with a description of the condition of *O. zophochir* and followed by a discussion of variations and specializations among other genera within the family. Also included in this section are discussions of the otoliths and of the gas bladder and digestive tract conditions of certain ophichthids.

*Ophichthus zophochir* was selected as the species with which other ophichthids are compared because it possesses the majority of ophichthid anatomical characters in a rather generalized state. This is not meant to imply that *O. zophochir* is the most primitive ophichthid, but rather

that by being generalized, and not specialized by means of extreme anatomical reduction, it provides a framework for comparison and discussion.

#### Neurocranium

The neurocranium of *O. zophochir* is completely ossified and well fused along the cranial sutures. The skull is stout, rather elongate, and truncate posteriorly. The neurocranium of an adult *O. zophochir*, like that of most anguilliforms, is small in relation to the total length of the fish. It occupies 5.5 percent of the TL, yet the neurocrania of more elongate ophichthids, such as *Phaenomonas cooperae*, occupy as little as 1.3 percent. Various aspects of the neuro-

cranium of *O. zophochir* are illustrated in figures 2 and 3. Described below are the elements composing the neurocranium.

*Premaxilloethmovomer.* The premaxillae, ethmoid, and vomer are fused into a single complex (PEV) articulating posterodorsally with the frontal and posteroventrally with the parasphenoid, and forming the anterior margin of the orbit. The anterior portion of the PEV, the premaxillae, has been shown to be separate from the vomer in other eels, including *Anguilla anguilla* (Norman, 1926), *Derichthys serpentinus* (Beebe, 1935), and *Coloconger scholesi* (Chan, 1967), yet in ophichthids there are no distinct sutures separating the elements, and their precise limits can only be determined ontogenetically. The premaxillary portion is expanded in most

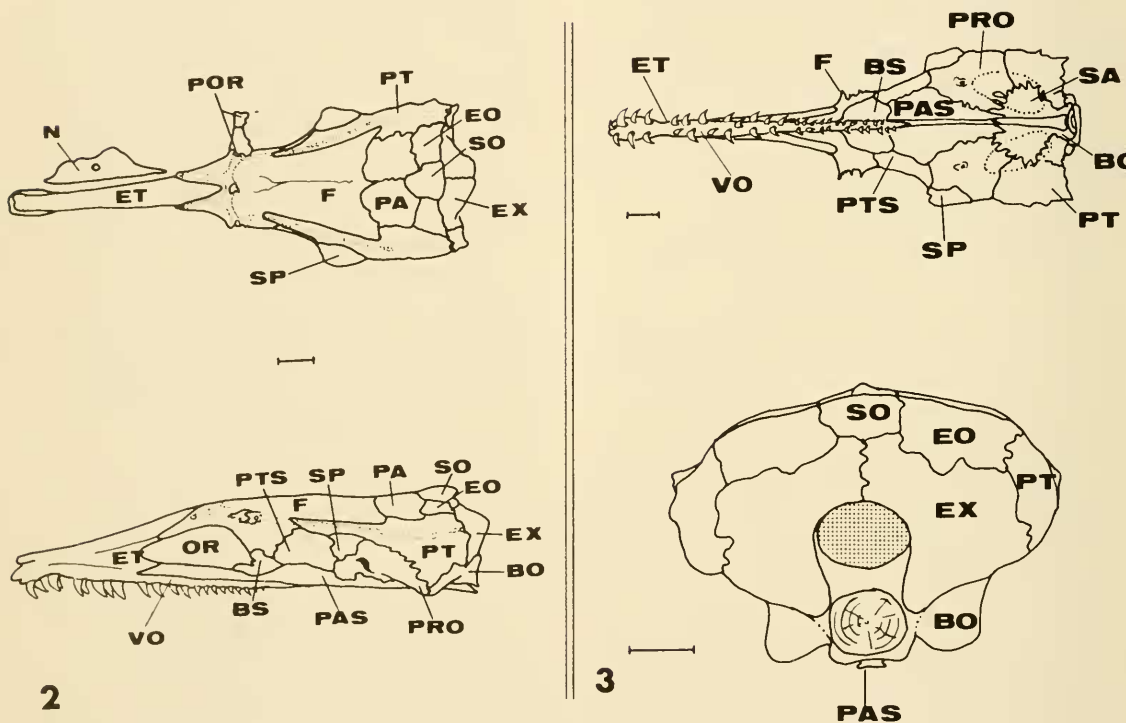
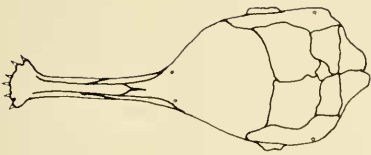
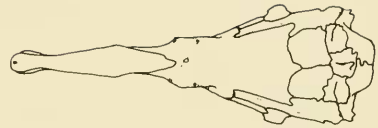


Figure 2. Neurocranium of *Ophichthus zophochir*, SIO 65-166. Upper, dorsal view; lower, left lateral view. Scale represents 1 mm. Stippled lines represent cephalic lateralis canals. Abbreviations are: BO, basioccipital; BS, basisphenoid; E, ethmoid portion of premaxilloethmovomer; EO, epiotic; EX, exoccipital; F, frontal; N, nasal; OR, orbit; PA, parietal; PAS, parasphenoid; POR, postorbitals; PRO, prootic; PT, pterotic; PTS, pterosphenoid; SO, supraoccipital; SP, sphenotic; VO, vomer.

Figure 3. Neurocranium of *Ophichthus zophochir*, SIO 65-166. Upper, ventral view; lower, posterior view. Scale represents 1 mm. Abbreviations are as in Figure 2. Sagitta (SA) is outlined by stippled line.



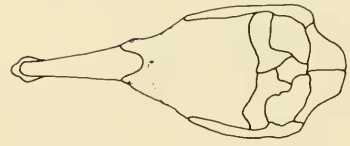
4



5



6



7

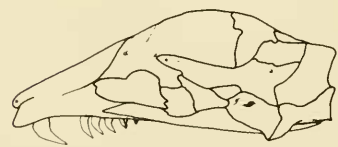


Figure 4. Neurocranium of *Benthenchelys cartieri*, DANA Sta. 3735. Scale represents 1 mm.

Figure 5. Neurocranium of *Myrophis vafer*, SIO 68-242. Scale represents 1 mm.

Figure 6. Neurocranium of *Muraenichthys chilensis*, SIO 65-655. Scale represents 1 mm.

Figure 7. Neurocranium of *Callechelys marmoratus*, SIO 69-629. Scale represents 1 mm.

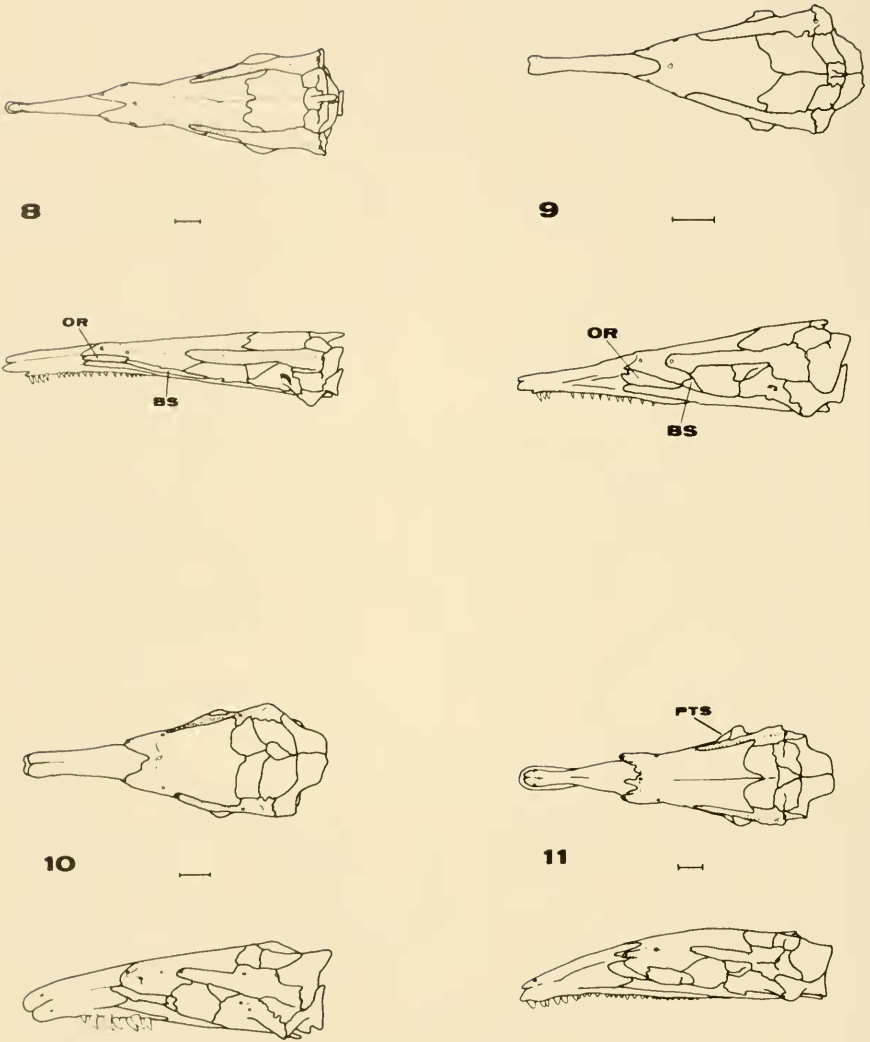


Figure 8. Neurocranium of *Ichthyapus selachops*, SIO 65-232. Scale represents 1 mm. Abbreviations are: BS, basisphenoid; OR, orbit.

Figure 9. Neurocranium of *Stictorhinus potamius*, MZUSP 8959. Scale represents 1 mm. Abbreviations are: BS, basisphenoid; OR, orbit.

Figure 10. Neurocranium of *Bascanichthys panamensis*, SIO 71-224. Scale represents 1 mm.

Figure 11. Neurocranium of *Myrichthys xystrurus*, SIO 65-335. Scale represents 1 mm. Abbreviation PTS is for pterosphenoid.

ophichthids (extremely so in *Benthenchelys*, fig. 4) and is toothed in all genera except *Aprognathodon*. It narrows posteriorly to become the vomer, which is toothed in most ophichthids (exceptions are *Schultzidia*, *Phyllophichthus*, *Leiuranus*, and *Leuropharus*). The premaxillary and ethmoid dentition, here termed intermaxillary, is continuous with that of the vomer in *O. zophochir*. A gap separates the intermaxillary and vomerine dentition of many ophichthid genera, and appears to be a useful character to indicate relationship (table 1). The vomerine dentition does not continue onto the parasphenoid. The ethmoid portion forms the anterior margin of the orbit and the medial margin of the nasals. The ethmoid is perforated anterolaterally by the lateral commissure of the first cranial nerve.

*Nasals*. The nasals of *O. zophochir* are paired, thin, laminar, and cartilaginous along their external edges. The anterior portion of the supra-orbital cephalic lateralis nerve tract passes through the canal along the median edge of the nasal. The nasals of the Myrophinae are either cartilaginous or absent. Nasal development among the Ophichthinae is variable. In certain long-jawed ophichthines (including *Brachysomphis*, *Scytalichthys*, and *Aplatophis*) the nasals are either rudimentary or absent. Nasal cartilage extends from the anterior edge of the PEV; its development is quite variable, generally consisting of two short lateral rods; in certain genera it is fused centrally.

*Parasphenoid*. The parasphenoid (PAS) is a long, narrow, toothless bone, anteriorly overlying the vomer and forming the ventral margin of orbit. Centrally, it is spread laterally to form the anterior floor of the cranium, narrows posteriorly, and splits into two short prongs. It forms the ventral margin of the orbit, and borders the orbitosphenoid, pterosphenoid, prootic, and basioccipital.

*Prootic*. The paired prootics (PRO) combine with the paired basioccipitals and pterotics to form the otic bulla. They are small, nearly rectangular, and highly perforated with numerous openings for the passage of nerves and blood vessels. Through the most conspicuous foramen passes the hyomandibular trunk of the facial nerve (VII). Smaller foramina exist for the passage of the orbital artery and the jugular vein. The major axis of the PRO is horizontal. The PRO are bordered by the parasphenoid medially, the pterosphenoid anteriorly, the sphenotic anterolaterally, the pterotic dorsolaterally, and the basioccipital posteriorly.

*Basioccipital*. The median basioccipital (BO) is a small, irregularly shaped bone which forms the posterior portion of the otic bulla. Its major axis, in contrast to the prootics, is vertical. It is bordered medially by the parasphenoid, anteriorly by the prootics, and dorsally by the pterotics and exoccipitals.

*Pterotic*. The paired pterotics (PT) are elongate, narrow anteriorly, and broadly flared laterally and posteriorly, forming the lateral edge of the roof of the cranium. The cephalic lateralis nerve tract passes through the PT and opens anteriorly in the frontal and posteriorly at the posterior PT margin. Anteromedially the PT are bordered by the frontal, followed medially by the parietals and epiotics, anterolaterally by the pterosphenoid and sphenotic, ventrolaterally by the prootic and basioccipital, and posteriorly by the exoccipitals. Posterior to the sphenotics, the PT forms a sheet-like eave extending beyond the body of the cranium.

*Exoccipital*. The paired exoccipitals (EX) form the dorsal and lateral margins of the foramen magnum. They are sutured along their dorsal midline, and extend posterodorsally and laterally as a semicircular sleeve around the foramen magnum. Ventrally, they contact the basioccipital, and dorsally the supraoccipital. The foramen of the tenth cranial nerve opens posteriorly along the ventral EX-BO border, with the ninth opening lateroventrally from a foramen slightly anterolateral to that of the tenth.

*Supraoccipital*. The supraoccipital (SO) is single, small, square to subrectangular in shape, and lies along the posterodorsal cranial midline. In *O. zophochir* the narrow median crest of the SO extends posteriorly as a small point. The condition is typical of many ophichthids, although in certain generic groups, particularly *Callechelys* and related genera, they are rounded along the posterior SO margin. The SO extends anteriorly beneath the parietals, and is bordered laterally by the epiotics, posteriorly by the exoccipitals, and anteriorly by the prootics in most genera. In *Schultzidia* the SO has surfaced and has separated the parietals, extending anteriorly to contact the frontal.

*Epiotic*. The epiotics (EO) are paired, thin, and subrectangular. In *O. zophochir* they are bordered anteriorly by the parietals, laterally by the pterotics, and medially by the supraoccipital. Posteriorly their major axis is changed from horizontal to vertical in forming the dorsolateral margin of the posterior cranial face bordering the exoccipitals. The EO, like the supraoccipital and

the pterotics, forms a narrow sheet-like eave along their posterior margins.

*Parietal.* The paired, thin, subrectangular parietals (PA) overlay the posterior margin of the frontal. They are bordered anteriorly by the frontal, laterally by the pterotics, posterolaterally by the epiotics, posteriorly by the supraoccipital, and fused medially. In certain ophichthids which have a prominent supraoccipital crest the median ridge development begins along the parietal midline and gradually increases to its posterior projection. Castle (1972: fig. 10) has erred in illustrating the PA of *Benthenchelys* as contacting the sphenotic; in no ophichthid did I find this juncture.

*Frontal.* The frontal (F) is a single long element which, along with the epiotics and parietals, forms the roof of the cranium. Ontogenetically, the frontal is presumably formed from the fusion of paired lateral elements, but in juveniles and adults there is no evident suture. In *O. zophochir* the F is ridged posteriorly along the dorsal midline. In *Aplatophis* this ridge is developed as a sharp crest. Several nerve tracts pass through the F, including the anterior tract of the cephalic lateralis nerve and the transverse frontal commissure, which is unique to the Ophichthidae. The frontal is deeply split anteriorly by the insertion of the ethmoid portion of the PEV in some genera, and bordered anteroventrally by the orbit and orbitosphenoid, ventrolaterally by the parasphenoid, laterally by the pterotic, and posteriorly by the parietals. The dorsalmost post-orbital of certain species of *Ophichthus*, *Echiophis*, and *Brachysomophis* is weakly sutured to the frontal at the level of the transverse commissure.

*Basisphenoid* (orbitosphenoid of others). The basisphenoid (BS) is a small, unpaired median bone with two lateral wings which forms the posteroventral margin of the orbit. It is bordered dorsally by the frontal, posteriorly by the pterosphenoids, and ventrally is supported by the parasphenoid (a myodome is not present). The BS in certain genera with elongate and depressed neurocrania has become narrow and elongate, as can be seen in a comparison of *Ophichthus* (fig. 2), *Ichthyapus* (fig. 8), and *Stictorhinus* (fig. 9).

Robins (1971: 164-165) has noted that the use of the term "orbitosphenoid" in other eel studies (including Gosline, 1950, 1951, 1952; Regan, 1912; Robins and Robins, 1967; Trewavas, 1932; and others) actually pertained to the BS. Chabanaud (1936) stated that the teleostean BS is not

homologous with that of higher vertebrates and proposed the name "porpital" for that bone in teleosts. Springer (1968: 43-44) agreed with Chabanaud's conclusions but conserved the name "basisphenoid" because of its widespread usage in ichthyology, an act with which I fully agree.

*Pterosphenoid* (=alisphenoid). The small paired pterosphenoids (PTS) form the anterodorsal roof of the cranium. In *O. zophochir* they are concave, turning evenly from a longitudinal axis (along the margin of the frontal) to a nearly transverse axis which abuts the anterior margin of the sphenotic. They are bordered anteriorly by the frontal, dorsally by the pterotics, posteriorly by the prootic and sphenotic, and medially by the parasphenoid. The conspicuous foramen along the PTS-pterotic border is the anterior opening of the trigemino-facialis chamber.

*Otoliths.* Ophichthid otoliths, like those of most anguilliforms, are small, and hence have received little attention either on a descriptive or a comparative basis. Studies are limited to those of Frost (1926), which included illustrations of the sagittae of *Myrus vulgaris* (= *Echelus myrus*), *Ophichthus gomesii*, and *Pisodonophis boro*, and the photograph of the sagitta of *Myrophis lepturus* in Kotthaus (1968). The sagitta (largest of the three otolith pairs) of twelve ophichthid species were compared in this study. The asteriscus and lapillus were too small to be of comparative value. Ophichthid otoliths are ovate and biconvex, with a shallow sulcus on the medial surface. They are particularly distinctive in having a shallow ostial channel which opens anteriorly rather than turning dorsally and opening from the sulcus, as is typical of the Congridae (cf. Frizzel and Lamber, 1962: fig. A; Frost, 1926: figs. 10-11, 15). The sagittae of *Ophisurus* and *Ophichthus* (fig. 12) possess a short anterior rostrum and are more elongate than those of *Ethadophis* and *Myrophis*, which are roughly circular. Sagittae of *Myrichthys* and *Echiophis* are intermediate in shape.

*Dentition.* Dentition has often been used as a principal character to define and differentiate ophichthid genera. The location and shape of teeth was found in this study to be an important indication of relationship. The dentition of *O. zophochir* represents the generalized ophichthid condition in being multiserial, conical, and on all tooth bearing bones (vomer, ethmoid, premaxilla, maxilla, and dentary). Considerable variation exists within the family, including the elongate fanglike dentition of *Aplatophis*, the molariform or granular dentition of *Myrichthys*,

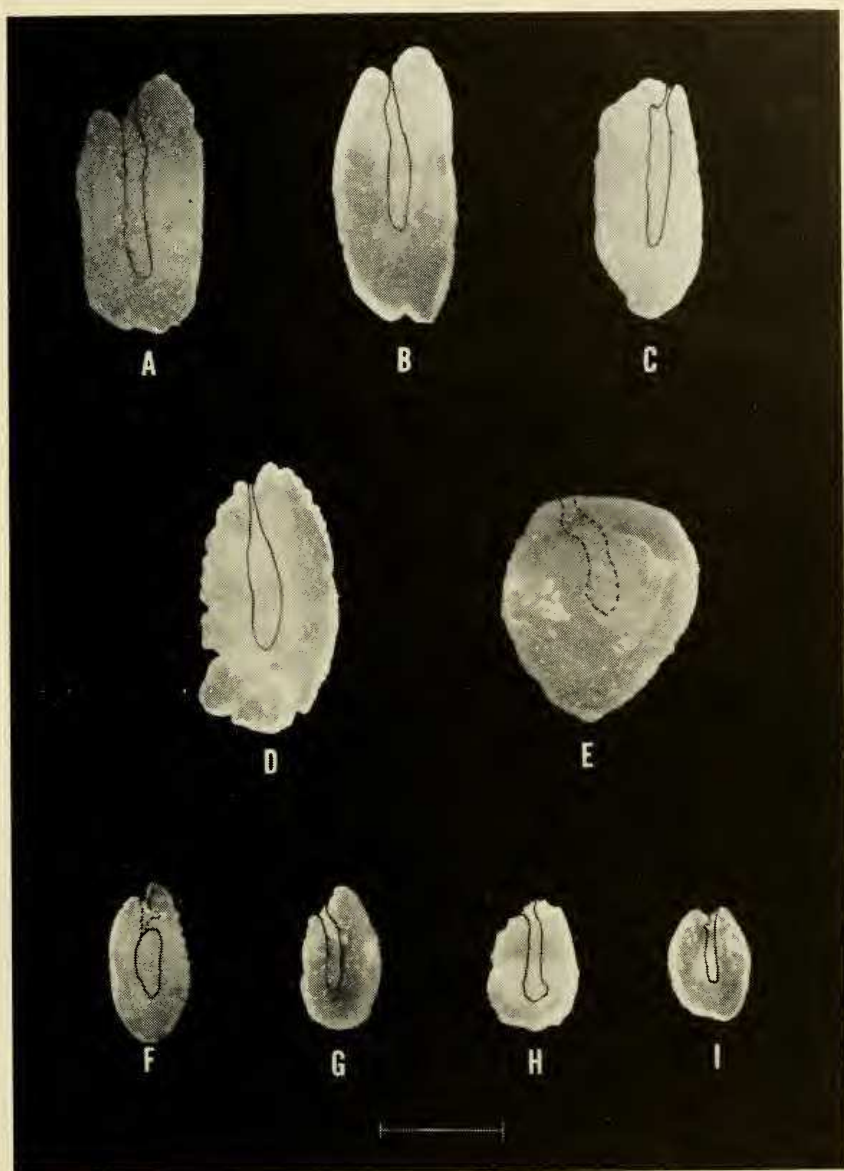


Figure 12. Otoliths (medial face, left sagitta) of several ophichthid species. Anterior end up. Sulcus outline inked in. Scale represents 2 mm.

A. *Ophichthus triserialis*

B. *Ophichthus zophochir*

C. *Ophisurus serpens*

D. *Echiophis intertinctus*

E. *Ethadophis merenda* (orientation uncertain)

F. *Myrichthys xystrurus*

G. *Echelus pachyrhynchus*

H. *Aplatophis chauliodus*

I. *Myrophis vafer*

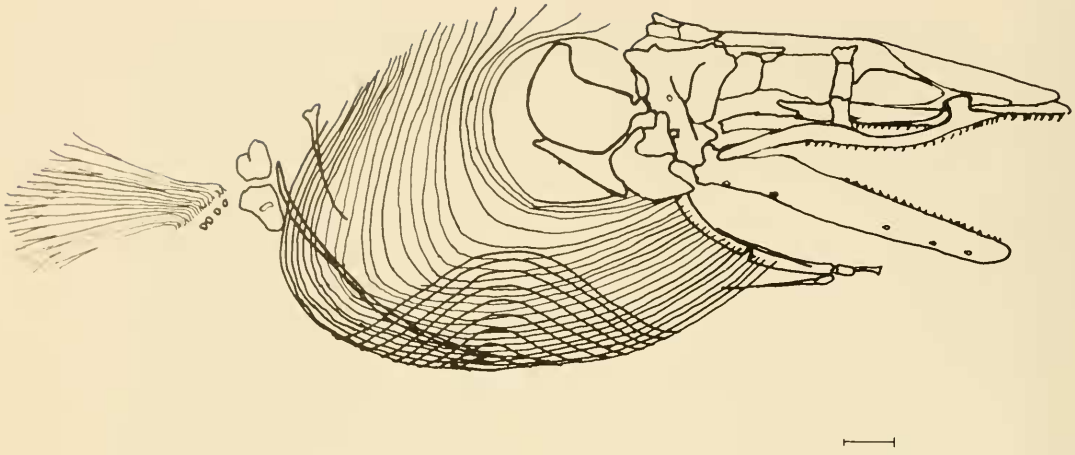


Figure 13. Head skeleton of *Ophichthus zophochir*, SIO 60-304. Scale represents 1 mm. Refer to Figures 2-3 (neurocranium), 14 (suspensorium), 17 (hyoid), and 19 (pectoral girdle) for names of bones.

*Pisodonophis* and certain species of *Muraenichthys*, the minute, nearly villiform dentition of *Schultzidia*, and the smooth toothless vomer of *Leiuranus*, *Leuropharus*, *Phyllophichthus* and *Schultzidia*. Characteristics of the dentition of ophichthid genera are summarized in table 1.

#### *Suspensorium and Jaws*

The conditions of the dentition, suspensorium, and jaws are directly related to the feeding habits of the various genera. In ophichthids, differences in feeding habits (e.g., major differences in prey items and adaptations of the predators to the different habitats) are greater between the species of different genera than between congeners. These differences are well evidenced in the form of the suspensorium and jaws of various ophichthids. The juxtaposition of the neurocranium, suspensorium and jaws, pectoral girdle and hyoid apparatus of *O. zophochir* is illustrated in figure 13.

All elements of the suspensorium and jaws are paired.

*Hyomandibular*. The hyomandibular (HYM) is stout and shaped like an inverted right triangle. The HYM of strong-jawed piscivorous genera is generally strongly ridged for the attachment of the massive adductor mandibularis muscle. The dorsal surface of the HYM abuts the sphenotic and pterotic. A small irregular condyle along the antero-dorsal margin of the HYM fits into a shallow socket formed along the sphenotic-pterotic suture. The large process on the posterior HYM

margin adjoins the anterior process of the opercle. The ventral portion of the HYM contacts the quadrate.

*Quadrate*. The small, stout quadrate (Q) is tightly sutured to the HYM. The vertical ridge along the outer face of the HYM is continuous along the Q. Ventrally the Q bears a broad rounded concave process that contacts the articular bone of the mandible.

*Articular*. The wedge-shaped articular (AR) is narrowed anteriorly, and slides into a pocket within the dentary. A remnant of the coronomeckelian is present along the inner face of the AR of *O. zophochir*; its presence in other genera was not systematically determined. Posteriorly, a grooved socket in the AR meets the rounded socket of the quadrate.

*Dentary*. The dentary (D) is the toothed bone of the mandible, joined by the articular posteriorly and adjoining its opposite member at the symphysis by a cartilaginous connection.

*Postorbitals*. The three postorbitals (POR) of most ophichthids are separate, weak ossicles that surround the nerve tract connecting the supra-orbital and infraorbital pore tracts. The POR of *O. zophochir* however, are specialized by enlargement and fusion to form a continuous strut bracing the mandible and neurocranium. This specialization, also present in other species of *Ophichthus* and *Echiophis*, is extreme in *Brachysomophis* (fig. 15).

The antorbital cartilaginous strut which Gosline (1952) described for *Echelus myrus* was not



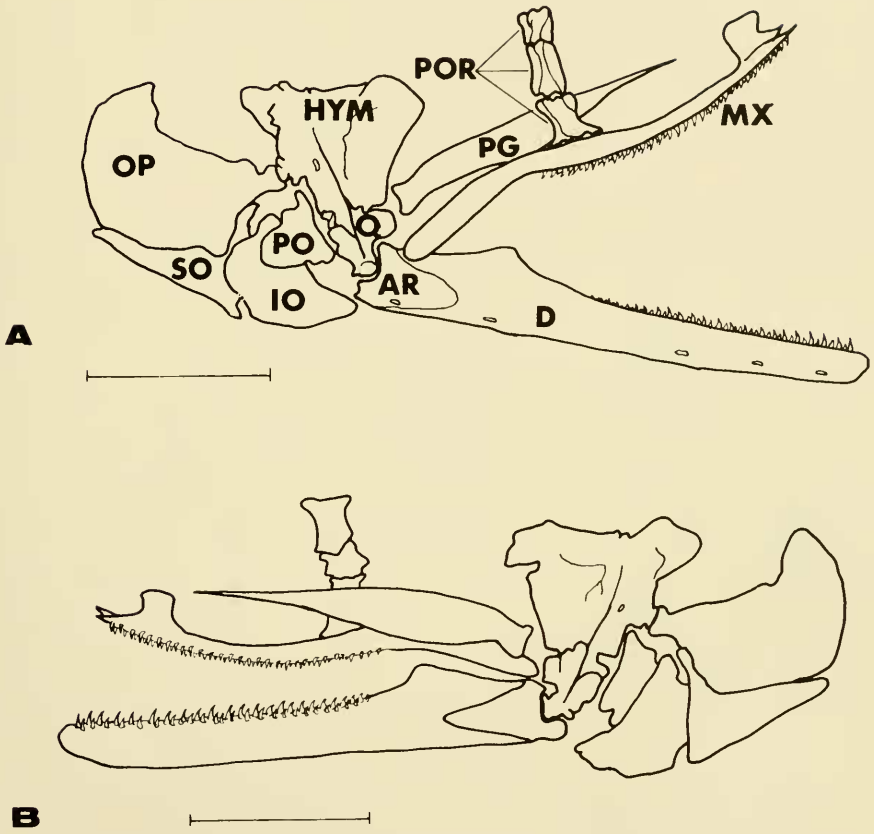


Figure 14. Suspensorium and jaws of *Ophichthus zophochir*, SIO 65-166. Scale represents 5 mm. Abbreviations are: AR, articular; D, dentary; HYM, hyomandibular; IO, interopercle; MX, maxilla; OP, opercle; PG, pterygoid; PO, preopercle; POR, postorbitals; Q, quadrate; SOP, subopercle.

A. Outer face

B. Inner face

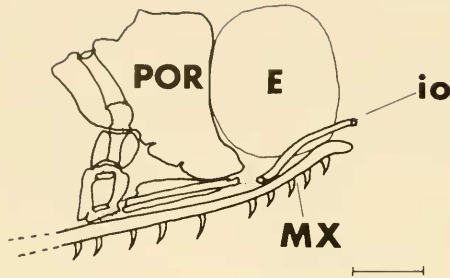


Figure 15. Right postorbital series of *Brachysomophis sauropsis*. Scale represents 1 mm. Abbreviations are: E, eyeball; MX, maxilla; POR, dorsal-most postorbital; io, infraorbital pore tract.

found in other ophichthids studied (see Remarks on *Echelus*). A similar cartilaginous strut has been observed in other eels however, including the dysommid *Atractodenchelys phrix* and in the Synphorbranchidae (Robins and Robins, 1970: 307). They felt "it (probably) represents either the pre-frontal or lateral ethmoid or their fusion."

*Pterygoid* (=palatopterygoid). Pterygoid (PG) development is variable within the family, although a clear pattern of relationship was not apparent. The PG is reduced to a narrow splint in most ophichthids. In *O. zophochir* it is thin, laminar, pointed anteriorly, and blunt posteriorly. It is held in place by the dermal layer and connective tissue, and contacts neither the quadrate nor the hyomandibular. The PG of all ophichthids tapers anteriorly, and often posteriorly, is largely cartilaginous in many species, and does not appear to serve any distinct purpose. *Ahlia* is exceptional in differing from the closely related species of *Myrophis* in the shape of its PG and in lacking vomerine teeth (fig. 30). A true palatine is not present in ophichthids, as shown by Robins and Robins (1971) in their discussion of the "palatopterygoid arcade."

*Maxilla*. The maxilla (MX) of all ophichthids is toothed, elongate, and possesses an anterior dorsal process which articulates with the PEV. Posteriorly, the maxillae of *O. zophochir* are truncate and do not extend beyond the articular. The generalized ophichthid condition however,

is that of a toothless, elongate, ossified or cartilaginous extension of the MX beyond and lateral to the articular. The location of maxillary articulation with the vomer is affected by the elongation of the snout and jaw, and is quite variable within the family. The condition is certain ophichthid genera is illustrated in figures 16 and 30.

In concluding this section on the neurocranium and suspensorium and jaws, certain comments are in order relating to their specializations and functional anatomy. Typical of the piscivorous adaptations of species of *Ophichthus*, *Brachysomophis*, *Echiophis* and related species are the strengthening provided by the cranial vault, the elongate pterotics, the broad junction of the hyomandibular along the neurocranium, and the bracing of the maxillae to the frontal by means of the fused postorbitals. An analogous condition exists in the muraenid genus *Gymnothorax*, in which a postorbital strut strengthens the jaws and suspensorium (cf. Burton, 1956: fig. 6). Other ophichthid genera, particularly among the Myrophinae and elongate ophichthines, are adapted to diets of minute invertebrate prey, and have extremely reduced neurocrania, suspensoria, jaws, and dentition.

#### *Opercular Series*

The opercular series of ophichthids, and of anguilliforms in general, is greatly reduced. This reduction is apparently related to the increase

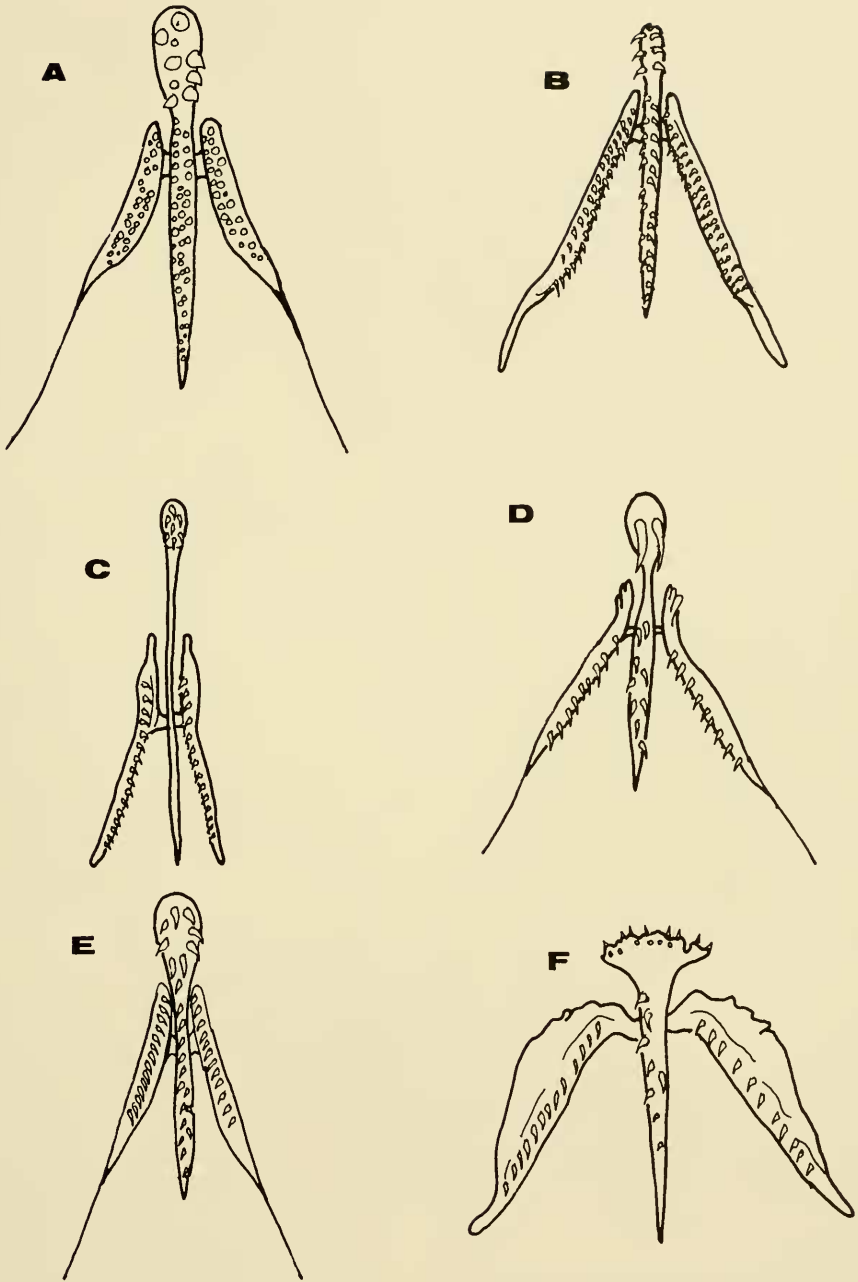


Figure 16. Maxillary-vomer apposition of several ophichthids. *Benthenchelys cartieri* enlarged 20 times, all others 9 times.

- A. *Myrichthys xysturus*
- B. *Ophichthus zophochir*
- C. *Phylloichthus xenodontus*

- D. *Callechelys marmoratus*
- E. *Muraenichthys chilensis*
- F. *Benthenchelys cartieri*

in number and importance of the branchiostegal rays as supporting elements for the branchial cavity (Greenwood, et al., 1966). Gosline (1959) has correlated the reduction of the opercular series, posterior displacement of the gill arches and pectoral girdle, and the separation of the pectoral girdle from the neurocranium with the peculiar branchial pump and circulatory mechanism of anguilliforms. Opercular reduction and deossification of cartilage, and the increase in the number of branchiostegals of ophichthids appear to be greatest in the smaller myrophines and elongate bascanichthyins and sphagebranchins. Within the Ophichthidae, the condition of *O. zophochir* closely approximates the generalized (primitive) state (fig. 14). The opercle (OP), the largest of the series, is posterior to the hyomandibular and above the subopercle (SOP), with its ventral margin lying lateral to the dorsal margin of the SOP. The interopercle (IO) overlays the SOP and is below the OP. The preopercle (PO), smallest of the series, overlays the (IO) and contains the tract of the preoperculo-mandibular nerve. The SOP and IO are the least ossified of the series, although the distal margins of most members of the opercular series are cartilaginous in most ophichthids.

Several specializations in each subfamily are useful indicators of phylogeny. For example, the SOP is produced posteriorly as a projection enclosing the ventral and posterior margins of the OP in species of *Myrophis* (fig. 33), *Ahlia*, *Muraenichthys* (Gosline, 1951a: fig. 3), *Pseudomyrophis*, and *Schismorhynchus*. This SOP-OP morphology is typical of other eel families, including certain Congridae (Asano, 1962; Rosenblatt, 1967), Moringuidae (Trewavas, 1932; Smith and Castle, 1972), Xenocongridae (Gosline, 1950, 1951b; Robins and Robins, 1967), and *Xenomyx atrarius* (Peden, 1972). The opercular series of *Callechelys* and related genera is reduced and has a conspicuously fringed appearance along the margin. The opercular series of *Stictorhinus*, *Apterichtus*, *Ichthyapus*, and related genera are quite reduced, with elements absent in certain genera.

#### Hyoid Apparatus

The hyoid apparatus and the associated branchiostegals provide fundamental characters which help to unify the subfamilies within the Ophichthidae. In particular, the broad overlap along the ventral midline of the branchial basket is herein considered a major phylogenetic character of the

family, not evidenced by homology or convergence in other eel families. The importance of this character, which later led to the combining of the Neenchelidae, Echelidae (in part), and the Ophichthidae, was recognized by Myers and Storey (1939), Gosline (1952), Bertin and Arambourg (1958), Böhlke (1960) and Nelson (1966b).

The general usage of the term "epihyal" in the ichthyological literature has been incorrect. As Goodrich (1930: 405-406) has pointed out, the true epihyal is homologous with the hyomandibular, and the element incorrectly termed the epihyal represents the posterior ossified element of the ceratohyal. I am in agreement with Goodrich's conclusions, however in view of its widespread usage in ichthyology, I have herein used the term "epihyal" to represent the posterior of the two ceratohyal elements, and the term "ceratohyal" for the anterior element.

The following description of the hyoid apparatus is based on that of *O. zophochir* (fig. 17A). The apparatus consists of the unpaired glossohyal (GH) and urohyal (UH), and paired upper hypohyals (HH), ceratohyals (CH), and epihyals (EH). The interhyal is absent. The outer posterodorsal margin of the EH is connected by cartilage to the inner face of the quadrate and provides support for the branchial basket. The CH and EH are connected by a stout cartilaginous strut affording little flexibility along the arch; further strengthening is provided by the flanking spike-like posterior extension of the CH along the outer edge of the EH. The GH is grooved along the posterodorsal half and extends forward as a small cylindrical teat. The GH and paired upper HH are interconnected by a weak cartilaginous plate. The upper HH is fused along a broad and slightly flexible suture to the CH. A ventrolateral extension of the CH braces the HH. The UH, lying ventrad to the HH, GH and CH, is flattened anteriorly and has a short cartilaginous connection from its anterior midpoint to the dorsoventral margin of the GH. Posteriorly, the UH extends as a slender ossified spike surrounded by a membranous sheath and overlays the branchiostegal rays. All the branchiostegal rays are inserted on the external face of the arch, 6 on the CH, 1 on the cartilaginous interspace, and 19 on the EH. The inner 3 and outer 9 rays are closely grouped basally and the remainder are more widely spaced. Rays 6-16 are expanded slightly at their bases but filiform for the remainder of their length. The rays broadly overlap along the ventral midline in a characteristic manner. The distal 19 rays of the left EH and cartil-

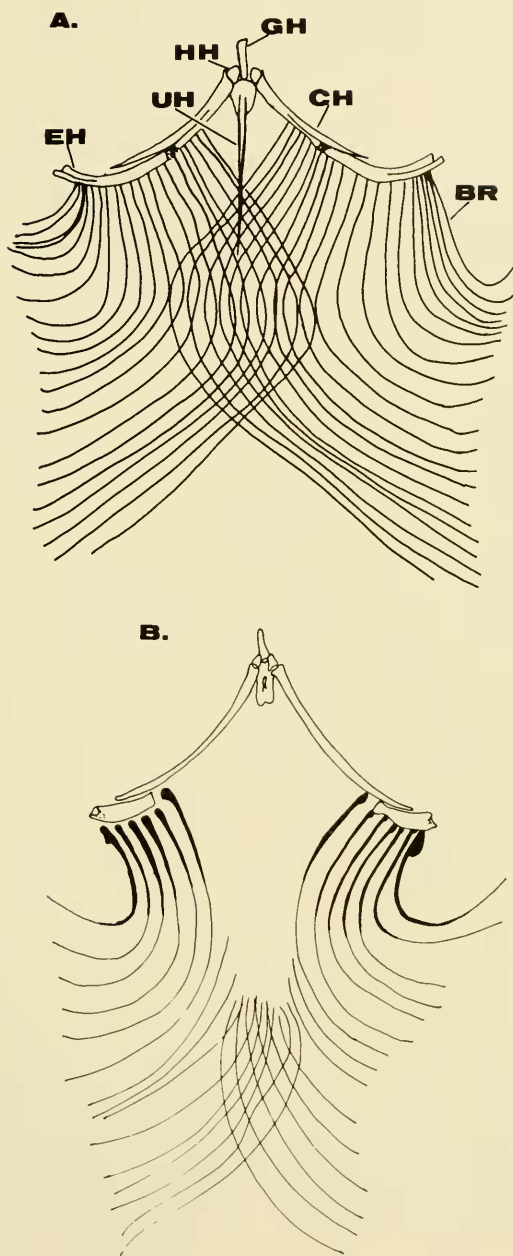


Figure 17. Hyoid arch and branchiostegals of *Ophichthus zophochir*, an ophichthine, and *Muraenichthys chilensis*, a myrophine. Dorsal view. Scale represents 1 mm. Abbreviations are: BR, branchiostegal rays; CH, ceratohyal; EH, epihyal; GH, glossohyal; HH, hypohyal; UH, urohyal.

A. *Ophichthus zophochir*

B. *Muraenichthys chilensis* (posterior-most branchiostegals not illustrated)

aginous interspace are overlain by all the rays of the right arch, which are in turn overlain by the remaining left CH rays. This pattern of the left CH rays overlaying the right CH and EH rays which overlap the left EH rays is consistent within the Ophichthidae.

The location and number of branchiostegal rays among the genera of ophichthids (table 2) and the proximity of the branchiostegal rays to the hyoid arch differs markedly in the ophichthid subfamilies. In the Myrophinae, which appear to follow the generalized anguilliform condition, the branchiostegal rays are attached to the outer face of the EH, often with a single ray on the CH (fig. 17B, *Muraenichthys*). The remainder of the branchiostegal rays, which will hereafter be referred to as the "accessory branchiostegal rays", are unattached and basally lie well behind the hyoid arch. In the Myrophinae, these vary from as many as 13 pairs in *Benthenchelys cartieri* to 42 pairs in *Myrophis vafer*. In the Ophichthinae, all branchiostegal rays are attached to the outer face of the hyoid arch (fig. 17A, *Ophichthus*), although in some species the rays have secondarily become detached.

The extreme development of this branchiostegal apparatus is obviously a means of strengthening the gill basket. The manner in which several ophichthines, particularly *Ophichthus*, *Echiophis*, *Brachysomophis*, and *Aplatophis* have all the rays attached to the face of the hyoid is probably related to a diet of struggling prey, in contrast to the myrophine condition of free rays and their diet of comparatively weak prey. The reduction of the opercular apparatus and the posterior displacement of the entire gill arch complex necessitates a supplementary skeletal framework to prevent the gill basket from collapsing during the normal burrowing activities of ophichthids. The posterior displacement of the gill arches among anguilliform families is extreme in the Ophichthidae and the Moringuidae (see Nelson, 1966a: fig. 58), both of which comprise predominantly sand and mud-burrowing forms.

The accessory branchiostegal apparatus of ophichthid and eelid eels was recognized by earlier workers, but Parr (1930) was the first to describe it and suggest its function. He created the term "jugostegalia" for the accessory skeleton of the gill cover in species of *Myrophis*. Because of their number he did not consider the attached rays to be homologous with the branchiostegals. In that the accessory rays are undifferentiable from the branchiostegal rays, especially in those ophichthine species in which all

rays are attached to the hyoid, I prefer not to use Parr's term, jugostegalia. Problems occur in the consideration of jugostegalia as a separate entity, even if one assumes them to be homologous with the branchiostegals. For example, in following Parr's concept of jugostegalia as those rays which are free from the hyoid, McAllister (1968: 85) stated that "*Myrichthys* (has) 28 (branchiostegal rays) plus 4 jugostegalia... *Myrophis* 5 plus 34-36 jugostegalia." McAllister's (p. 80) retention of the term jugostegalia "for those secondarily multiplied, overlapping and free branchiostegals found in certain anguilliforms" is inadequate as seen in the above usage. I therefore propose that a more flexible terminology be applied to those rays, and prefer the term "accessory branchiostegal rays".

The branchiostegal rays also reflect intrageneric and intergeneric similarities through their basal thickening and secondary multiplication. The outermost rays of all myrophines and several ophichthines are proximally broadened (e.g., *Muraenichthys*, fig. 17B, and *Neenchelys*, Nelson, 1966b: fig. 2a). This condition is similar to the general anguilliform condition as displayed by congrid, muraenids, anguillids, and other apodal families. In other ophichthines, particularly *Ophichthus*, *Aplatophis*, *Myrichthys*, and *Quassiremus*, the branchiostegals are filiform throughout. The basal splitting or secondary multiplication of the few inner and outermost rays is probably secondarily related to the number and spacing of the rays along the arch. For example, in species of *Echiophis* and *Ophisurus* the branchiostegals on the CH are paired, and are often fused at their bases. No trends were apparent in this condition within the Ophichthidae, hence it appears to be of limited value as a phylogenetic indicator.

The urohyal of most ophichthines is produced posteriorly as an ossified spike. The UH of all myrophines is limited to an ossified basal plate with cartilaginous posterior filaments. The few ophichthines that lack the ossified spike are clearly derived from the generalized condition typified by *Ophichthus*, rather than from the somewhat similar myrophine condition. A cursory survey of other eel families indicates that the ophichthine condition is primitive in relation to the more specialized myrophine condition.

A major subfamilial difference is also evidenced in the ceratohyal. Without exception, the CH of the Ophichthinae is split into an elongate and pointed distal portion and a shorter, truncate medial portion which connects, by means of

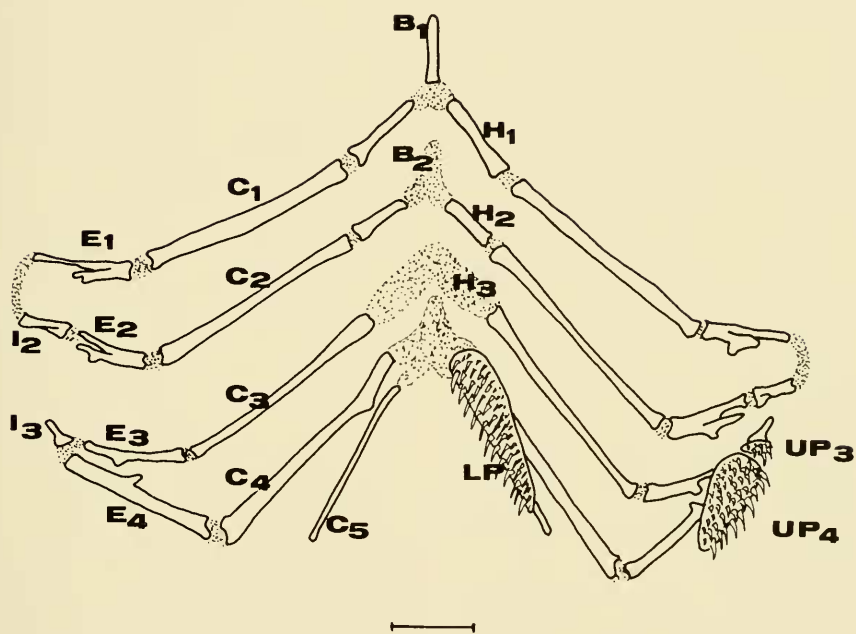


Figure 18. Gill arch skeleton of *Ophichthus zophochir*, SIO 65-166. Dorsal view. Gill arches have been cut along the dorsal midline and spread laterally; left upper and lower pharyngeal tooth plates are removed to show underlying bones. Stippling indicates cartilage. Scale represents 1 mm. Abbreviations are: B<sub>1</sub>, first basibranchial; C<sub>1</sub>, first ceratobranchial; E<sub>1</sub>, first epibranchial; H<sub>1</sub>, first hypobranchial; I<sub>2</sub>, second infrapharyngobranchial; LP, lower pharyngeal tooth plate; UP<sub>3</sub>, upper pharyngeal tooth plate.

cartilage, with the EH (fig. 17A). The myrophine CH is not split, but is rather a simple bowed bone, distal to, and terminating at about the midpoint, of the EH. The myrophine condition appears to involve a unique reduction, whereas the ophichthine condition is similar to that of the Congridae (Asano, 1962; D. Smith, 1971; Rosenblatt, 1967) and other eel families.

The hypohyals of most ophichthines are like those of *O. zophochir*. In certain otherwise dissimilar genera, including *Schismorhynchus*, *Aprognathodon*, and *Phyllophichthus*, the HH are absent. Careful examination of the anterior end of the CH did not reveal a suture or line of fusion, so it might be assumed that the HH are lost altogether. Observation of an ontogenetic series might provide proof of fusion or absence.

#### Gill Arches

Certain elements of the anguilliform gill arch skeleton have been shown to be important indicators of phylogeny (Nelson, 1966a). The Ophichthidae differ from all other eel families in a combination of gill arch characters, including: a cartilaginous connection between the proximal ends of the dorsal part of the first and second gill arches (according to Nelson, peculiar to the Ophichthidae); first basibranchial either ossified or absent, all others cartilaginous, rudimentary, or absent; hypobranchials 1-2 ossified; second infrapharyngobranchial ( $I_2$ ) ossified. If one considers the anguillid or congrid gill arch conditions, that of numerous ossified elements with minor loss or reduction, to be primitive among the anguilliforms, then the ophichthids are considerably advanced in having several osseous elements replaced with cartilage, and in having others reduced or entirely lost. Extending this supposition within the Ophichthidae, the Ophichthinae, and in particular the Ophichthini, are more primitive than the Myrophinae, which have lost the fifth ceratobranchial ( $C_5$ ) and have reduced or lost certain basibranchials (tables 3-4). The ophichthids are also specialized in having the gill arch skeleton displaced posteriorly in relation to the cranium. Among shallow-water eel families this condition is exceeded only in the Moringuidae (see Nelson, 1966a: fig. 58). References to gill arches of ophichthid species are limited to Popta's (1904) pioneering study of apodal gill arches (which treated *Muraenichthys gymnopterus*, *Leiuranus semicinctus*, *Caecula polyophthalmus*, *Pisodonophis boro*, and *Myrichthys colubrinus*), Nelson's (1966a) detailed

study, which included species from 18 ophichthid genera, and Nelson's (1966b) treatment of *Neenchelys buitendijki*.

The following description of the gill arch system of *Ophichthus zophochir* (fig. 18) illustrates the presumably primitive condition within the Ophichthidae. Terminology of gill arch elements follows that of Nelson (1969: 480). The basibranchials are single elements, not interconnected, lying along the ventral midline; all other gill arch elements are paired. The first basibranchial is ossified, slender, and connected by cartilage to the first hypobranchials. Basibranchials 2-4 are cartilaginous and connected to the adjoining hypobranchial pair. Hypobranchials 1-2 are ossified and stout. Hypobranchials 3-5 are cartilaginous, with 4 and 5 fused. Ceratobranchials 1-4 are ossified and subequal. Ceratobranchial 5 is reduced to a slender filament which is fused for most of its length with the ventral surface of the ventral pharyngeal tooth plate. Epibranchials 1-4 are short, stout, and bear various processes for cartilaginous or ligamentous attachment. The first infrapharyngobranchial ( $I_1$ ), as in all eels, is absent. The second connects to the first epibranchial by a cartilaginous strap; this condition, as mentioned earlier, is peculiar to all ophichthids. The third is "T" shaped and distally supports the third upper pharyngeal tooth plate ( $UP_3$ ). The upper pharyngeal plates are separated by a suture, the third being much smaller than the fourth ( $UP_4$ ). Each plate bears along one margin a single row of slightly retrorse conical teeth which grades to a fine-toothed pavement. *In situ*, the tooth plates overlie each other, and surround the esophageal canal so that the corresponding toothed areas of the upper and lower plates are aligned.

The third hypobranchial is cartilaginous in nearly all ophichthids. This specialization probably functions to increase the flexibility of the gill arch skeleton and, in particular, to allow further anterior movement of the lower pharyngeal tooth plates. For the same reason the fourth hypobranchial is never ossified. The species with ossified third hypobranchials, *Dalophis imberbis*, *Aprognathodon platyventris*, and *Elapsopsis cyclorhinus*, are highly specialized and not closely related. Two examples of each of the latter two species were examined to rule out the possibility of anomalous specimens. Both specimens of *Elapsopsis* had a well ossified  $H_3$  pair, and slender, nearly subequal tooth plates bearing conical biserial teeth. The two specimens of *Aprognathodon* were somewhat aberrant in the



H<sub>3</sub> condition. In one, the left H<sub>3</sub> was well ossified but the right was cartilaginous. The other had small discontinuous pieces of bone lying within a cartilaginous matrix on both sides. In both specimens the short, stout H<sub>1-2</sub> pairs nearly met along the ventral midline, and the small tooth plates bore several slender pointed teeth. In these exceptional species there has probably been a return to an ossified H<sub>3</sub> condition rather than a retention of the primitive ancestral ophichthid condition, possibly related to a specialized diet which would require less flexibility in the gill arch skeleton.

Microscopic examination and interpretation of the gill arch elements is often difficult, particularly in differentiating the rudimentary and cartilaginous conditions of the basibranchials. Nelson (1966a: 393), for example, considered the fourth basibranchial condition of *Leiuranus semicinctus* and *Machaerenchelys phoenixensis* to differ, although most authors have regarded the latter species as a color variant synonymous with the former species. The interpretation of the UP<sub>3</sub>-UP<sub>4</sub> fusion also tends to be subjective and is not heavily relied upon. Since anomalies often occur in the gill arch skeleton, duplicate specimens were examined in this study when suspicious results were encountered.

Nelson (1966a) identified certain ophichthid lineages on the basis of the gill arch conditions. These comprised (a) those genera with a moderately well-developed series of basibranchials and an ossified fifth ceratobranchial, (b) those with C<sub>5</sub> reduced or cartilaginous, and (c) those with very reduced basibranchials and lacking C<sub>5</sub>, i.e., the Myrophinae. Nelson erred in considering *Echelus myrus* to be an echeline (=myrophine) but did recognize the generalized condition of its basibranchials and C<sub>5</sub>. My study has shown Nelson correct in his other interpretations and now places other genera within his general framework.

The functional significance of the modification of the gill arches in apodal fishes was discussed by Nelson (1966a). The posterior displacement of the gill arches, the reduction and modification of osseous elements, and the absence of a firm interconnection with the cranium has transformed their function from prey catching (now left to the jaws and cranium alone) to one of moving large food items through a secondarily elongated pharynx. As Nelson (p. 404) has pointed out, "many of these same modifications have occurred independently among syngnathiform fishes and sybranchiform fishes . . . , pos-

sibly also as a result of spatial separation of jaws and gill arches."

#### *Pectoral Girdle*

The pectoral girdle varies considerably within the Ophichthidae, grading from a well developed to a reduced condition in both subfamilies. The primitive condition, represented by *Ophichthus* (fig. 19A) in the Ophichthinae and by *Myrophis* in the Myrophinae (figs. 20E-F), includes the retention of the cleithrum (Cl), supracleithrum (SCL), scapula (=hypercoracoid) (Sc), and coracoid (=hypocoracoid) (Co), and in the Ophichthinae, the actinosts. The posttemporal is absent and the pectoral girdle is not attached to the cranium in anguilliforms (Gosline, 1971). The pectoral fin is best developed in genera such as *Ophichthus*, *Echelus*, *Echiophis*, *Mystriophis*, *Ap-latophis*, *Malvoliophis*, *Cirrhimuraena*, *Pisodonophis*, and *Pogonophis* in the Ophichthinae, and *Myrophis* and *Ahlia* in the Myrophinae. The pectoral fin rays are in some cases (*Ahlia* and *Myrophis*) multiply-branched. Pectoral rays vary in number from three to four weak stubs in *Bascanichthys panamensis* to 18 rays in *Pogonophis fossatus*.

The coracoid and scapula generally lie within a cartilaginous plate which provides a rigid support for pectoral fin movement. When present, the pectoral fin base lies in a dorsoventral plane and is broad-based in relation to the fin length (extremely so in *Myrichthys*), offering little rotational movement. Observations of live *Echiophis* sp. and *Ophichthus triserialis* indicate that those ophichthines use their pectoral fins to assist the body musculature in making short darting movements during feeding. Observations of live *Bascanichthys panamensis* suggest that the highly reduced pectoral fin serves little, if any, locomotory function. In those forms lacking pectoral fins, the cartilage, as well as the Co and Sc, is reduced or absent entirely. The trend in pectoral girdle reduction is related to the burrowing habit of many ophichthids. The primary function of the pectoral girdle as the structural support for the pectoral fin has in burrowing forms become one of structural support for the posterior end of the branchial basket. In no species are all girdle elements absent, but in *Cirricaecula* (fig. 19N) and in species of *Ichthyapus* only the Cl remains, and in species of *Muraenichthys* the Cl is a thin curved bone which is nearly identical in appearance and in function to the last of the accessory branchiostegals. The SCL of several

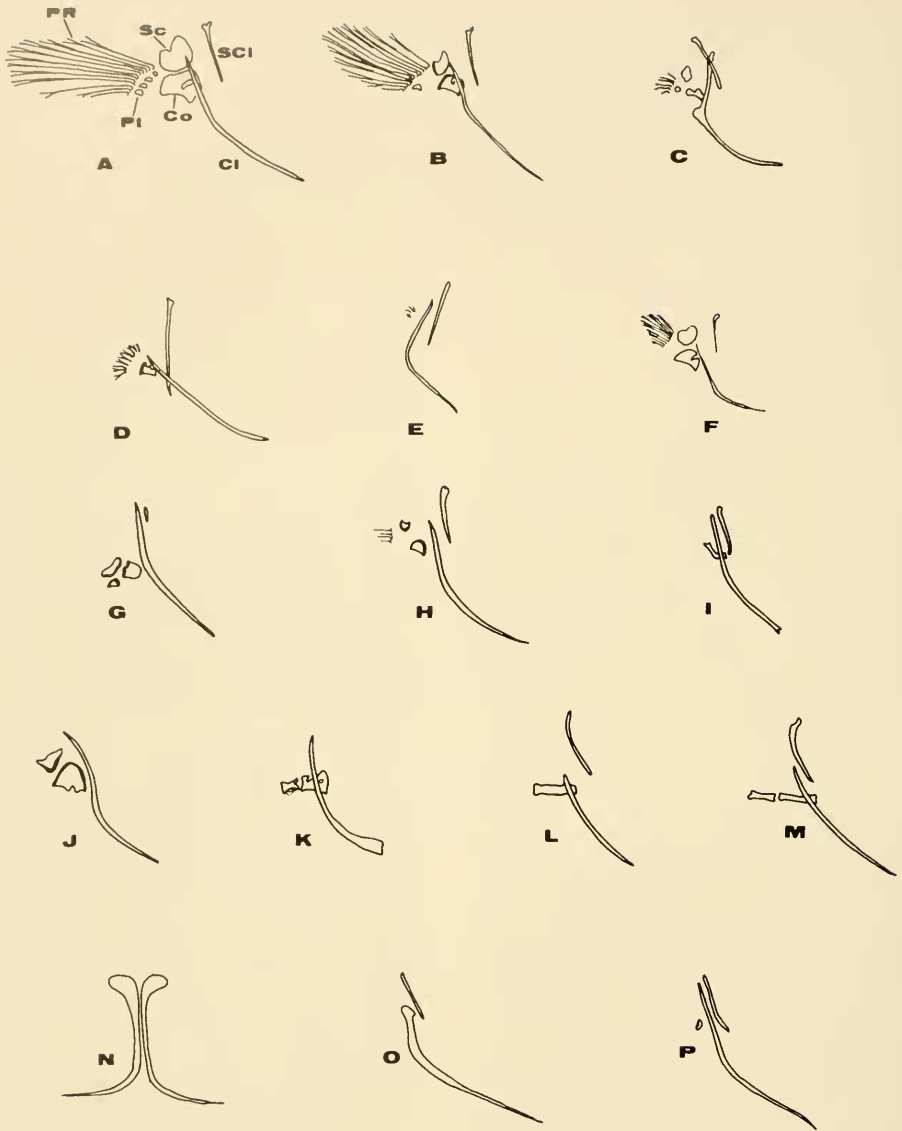


Figure 19. Pectoral girdle of various representative ophichthine genera. All are shown in lateral view, right side, except *Cirricaecula* which is viewed ventrally. Abbreviations are: Cl, cleithrum; Co, coracoid; PR, pectoral rays; Pt, pterygiophores; Sc, scapula; SCI, supra-cleithrum.

- |                                    |                                      |
|------------------------------------|--------------------------------------|
| A. <i>Ophichthus zophochir</i>     | I. <i>Phaenomonas pinnata</i>        |
| B. <i>Pisodonophis boro</i>        | J. <i>Caecula pterygera</i>          |
| C. <i>Elapsopsis cyclorhinus</i>   | K. <i>Lamnostoma orientalis</i>      |
| D. <i>Myrichthys xystrurus</i>     | L. <i>Callechelys marmoratus</i>     |
| E. <i>Quassiremus nothochir</i>    | M. <i>Aprognathodon platyventris</i> |
| F. <i>Aplatophis chauliodus</i>    | N. <i>Cirricaecula johnsoni</i>      |
| G. <i>Caralophia loxochila</i>     | O. <i>Apterichtus flavicaudus</i>    |
| H. <i>Bascanichthys panamensis</i> | P. <i>Yirkkala tenuis</i>            |

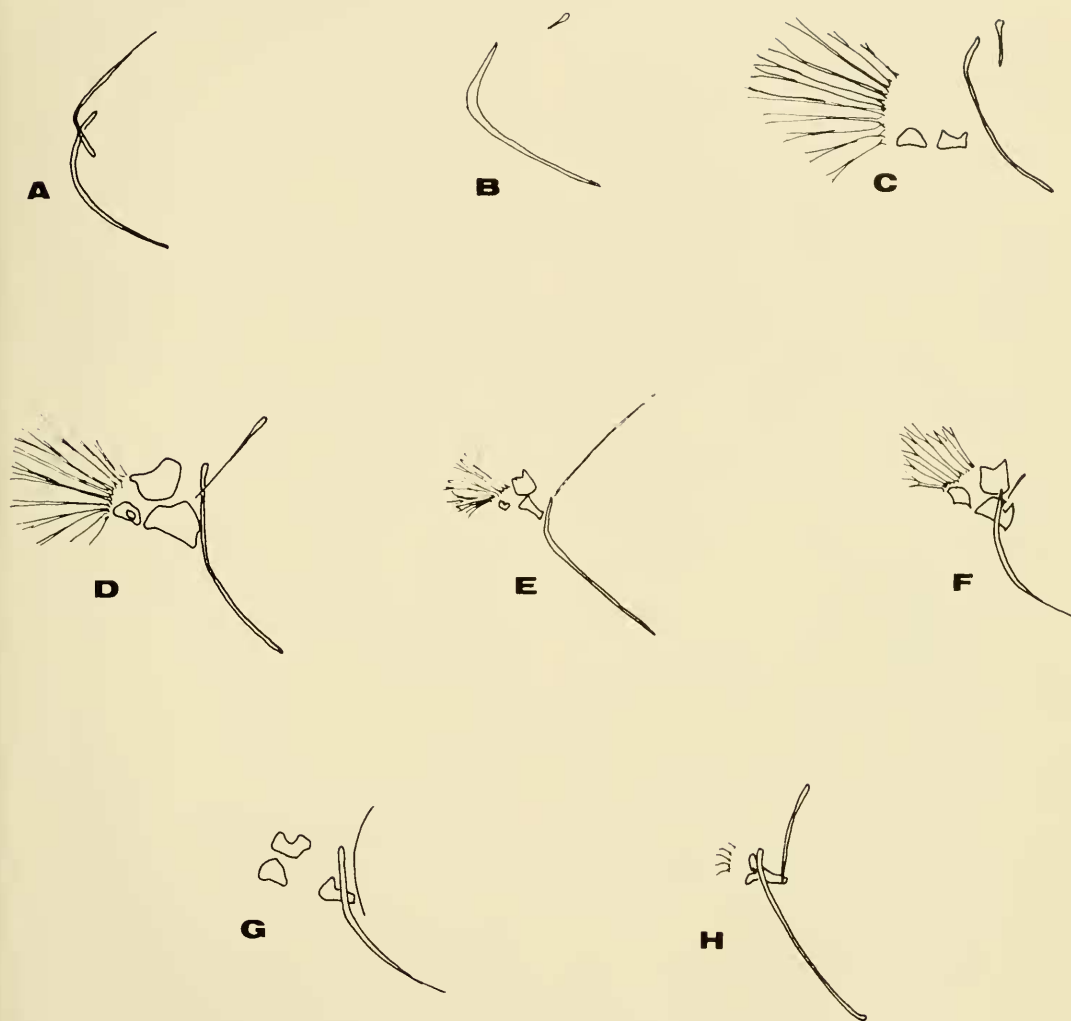


Figure 20. Pectoral girdle of various representative myrophine genera. All are shown in lateral view, right side.

- A. *Muraenichthys gymnopterus*
- B. *Muraenichthys chilensis*
- C. *Benthenchelys cartieri*
- D. *Ahlia egmontis*
- E. *Myrophis vafer*
- F. *Myrophis uropterus*
- G. *Neenchelys buitendijki* (from Nelson, 1966b: fig. 2c), pectoral fin rays not illustrated
- H. *Pseudomyrophis micropinna*

species of *Muraenichthys* is merely a thin sliver (e.g., *M. chilensis*, fig. 20B) and it is lost altogether in *Schismorhynchus*.

A peculiar Co and Sc condition exists in the Callechelyini and several of the Bascanichthyini, representing a unique ophichthid specialization which is not seen in other apodal fishes. It is nearly universal among eels for the Sc to be a nearly round bone (flattened slightly on the posterodorsal edge) lying above the Co (also nearly round but slightly flattened on the posteroventral edge), one or both of which are fenestrated. This is also the generalized ophichthine and myrophine condition. The Callechelyini possess either one or two small rod-shaped bones which are connected by cartilage and are oriented horizontally in the normal location of the Co (see *Aprognathodon*, fig. 19M and *Callechelys marmoratus*, fig. 19L). Species of *Phaenomonas* and *Ethadophis*, and the sphagebranchin *Lamnostoma orientalis* are similar in this condition. The homologies of these two rod-shaped bones are not entirely clear, but until further evidence is discovered, I will consider the anterior bone to be homologous with the Co and the posterior one to be homologous with the Sc. Pectoral girdle reduction in *Myrichthys* provides an indication of its generic homologies, particularly to species of *Pisodonophis*. The Sc in all species of *Myrichthys* is lost and the Co has lost its dorsal curvature (see fig. 19D). This condition is also that of *Pisodonophis daspilotus*, a species clearly more similar to other *Pisodonophis* than to species of *Myrichthys* in other osteological characters. Further similarities in all species of both genera include the shape of the Cl and SCl. Other *Pisodonophis* examined have retained the Sc and a complete Co, a condition more like that of *Ophichthus*.

The ancestral condition of those genera which entirely lack the Co and Sc is not indicated by remnants of cartilage or bone or transitional species, and is therefore indeterminable. The loss of the Co and Sc in *Ichthyapus*, *Apterichthys*, *Cirriacaecula* and *Quassiremus* may have been independent, although the first three genera are related on the basis of other characters.

#### Lateralis System

The apodal lateralis system and associated bones have been shown to be useful indicators of relationship, particularly within the Congridae (Asano, 1962; D. Smith, 1972). Asano showed that the number of pores within the cephalic

canal vary within and between genera of Japanese congrids. The lateralis system within the Ophichthidae was found to differ in a characteristic manner at the subfamilial and tribal level. It is best developed in the Ophichthinae and reduced in the Myrophinae. The ophichthid lateralis system has been described and illustrated on several occasions, usually on a species by species basis and not in a comparative manner. These works include: Allis (1903), *Ophisurus serpens* and *Echelus myrus* (as *Myrus vulgaris*); Gosline (1951a), *Ichthyapus vulturis* (as *Caecula platyrhyncha*); Hopkirk (1965), *Ophichthus zophochir*; Nelson (1966b), *Neenchelys buitendijki*; Blache (1968), *Echelus myrus*, *E. pachyrhynchus* and *Myrophis plumbeus*; Blache (1971), *Mystriophis rostellatus*, *M. crosnieri*, and *Echiophis intertinctus*; and Blache and Cadenat (1971), *Myrichthys pardalis*, *Bascanichthys* spp., and *Callechelys* spp.

The ophichthid lateralis system is divisible into seven canals: lateral line, supraorbital, infraorbital, preoperculomandibular, temporal, supratemporal commissure, and frontal commissure. The canals lie either within certain cephalic bones (frontal, pterotic, nasal, preopercle, postorbital, and dentary) or weakly ossified tubes (ossicles) which are broken at short intervals to provide flexibility. The Ophichthidae are distinctive in having the right and left sides of the cephalic lateralis system connected through the frontal and temporal canals.

The following description of the lateralis system of *Ophichthus zophochir*, a species which shows little reduction and minor specialization, illustrates the general ophichthine condition (fig. 21). The supraorbital canal connects with the infraorbital and temporal series posteriorly, and with its opposite member dorsally across the transverse frontal commissure. A single median supraorbital pore is present. Three supraorbital pores are associated with the nasal, the central pore lying within that bone. The anteriormost ethmoidal pore is connected to the supraorbital canal by a short cartilaginous connection. There are six infraorbital pores. Four lie horizontally beneath the eye in an ossified canal posterodistally overlying the maxilla, followed by two vertical pores lying behind the orbit and connected to a canal passing through the three postorbital bones. The supraorbital canal connects posteriorly with the temporal canal and commissure, passing through the frontal and pterotics. A single median supratemporal pore is flanked laterally by a pore on each side. The temporal

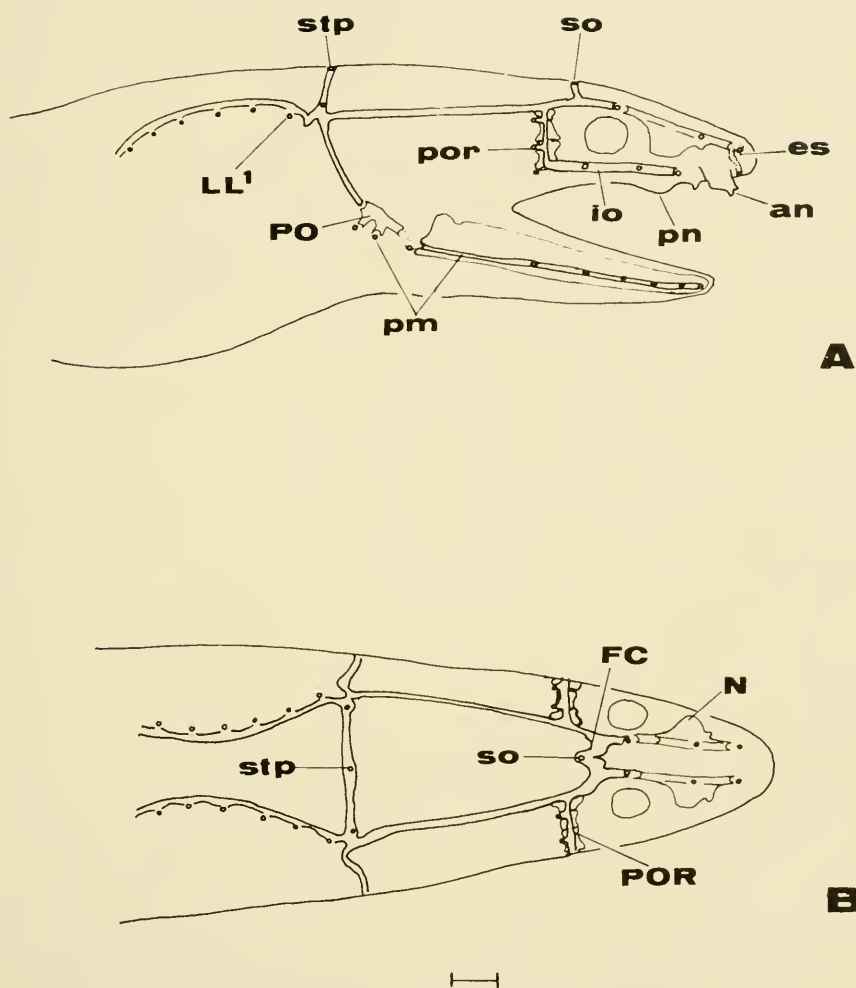


Figure 21. Cephalic lateralis system and associated bones of *Ophichthus zophochir*, SIO 60-309. Stippling indicates cartilaginous canal section. Scale represents 1 mm. Abbreviations are: an, anterior nostril; es, ethmoid section of supraorbital pores; FC, transverse frontal commissure; io, infraorbital pores; LL<sup>1</sup>, anteriomost lateral line pore; N, nasal bone; pm, preoperculomandibular pores; pn, location of posterior nostril; PO, preopercle; por, postorbital pores; POR, postorbital bones; so, supraorbital pore; stp, supratemporal pore.

A. Right side view

B. Dorsal view

canal extends posteriorly to the lateral line canal and ventrally to the preoperculomandibular canal. The preopercular section connects by an ossified tube to the preopercle, with two ventrolateral pores passing from the bone. A cartilaginous connection with the third preopercular pore joins the preopercular and mandibular sections. By overlying the quadrate and angular-articular juncture this cartilaginous connection provides the flexibility necessary during jaw movement. The seven pores comprising the mandibular series are unevenly spaced along the dentary. The lateral line (LL) canal extends posteriorly from the preoperculomandibular-temporal canal juncture, loops above the branchial basket, and continues midlaterally to within 0.2 head length of the tail tip. There are approximately 150 LL pores, 51 of them before the anal origin. Lateral line ossicles are moderately ossified, separated at each pore, and open along the distal margin (fig. 22F). On the medial face of all LL ossicles there is a centrally located opening for the nerve. Lateral line ossicle development is reduced posteriorly and absent before the last few caudal pores.

Suprageneric relationships among ophichthid genera are indicated by repeating pore patterns in certain cephalic canals, particularly in the preopercular portion of the preoperculomandibular canal and in the temporal canal (table 5). The generalized ophichthine condition consists of three preopercular pores and a single temporal pore on either side of the median supratemporal pore (as in *Ophichthus zophochir*, Fig 21, and *Ophisurus serpens*, Fig. 24B). The third preopercular pore ( $pop^3$ ) is lost in certain Ophichthini and all Callechelyini and Bascanichthyini. Certain Sphagebranchini are specialized in having a fourth preopercular pore ( $pop^4$ ) and a second temporal pore ( $tp^2$ ), as in *Ichthyapus selachops* (fig. 24A). This condition is not uniform throughout the Sphagebranchini, and may vary between and within populations, as evidenced by isolated populations of *Ichthyapus vulturis* (Randall and McCosker, 1975). The Myrophinae lack  $tp^2$  and  $pop^4$ . The  $pop^3$  is present in *Ahlia*, *Myrophis*, *Pseudomyrophis*, *Muraenichthys*, and *Schismorhynchus*, but is absent in *Neenchelys*, *Schultzidia*, and *Benthenchelys* (see Nelson, 1966a, figs. 21-25, in which *Schismorhynchus* was called *Leptenchelys labialis*, and Nelson, 1966b, fig. 1a).

The lateral line ossicles also indicate relationship in their degree of ossification, separation at each pore, and the pore position along the canal. Most pores lie below the midline of the

LL canal, although some genera are specialized in having the pores located centrally within the canal. Lateral line ossicles are nearly solid structures in the Sphagebranchini and Callechelyini, less substantial in the Ophichthini, and most reduced in the Myrophinae (figs. 22-23).

Certain genera of the Ophichthini are specialized in having a well-developed free sensory neuromast system along the sides and top of the head. The elaborate development of these sense organs has been generally overlooked. The neuromasts are not randomly scattered across the head region, but tend to follow distinct patterns. Nelson (1972) identified these lines of papillae in esocids as "pitlines", which are apparently homologous to the free sensory neuromasts described herein. Following his terminology, the neuromast lines of *Ophisurus serpens* (fig. 24), beginning at the snout tip, include paired subnasal, antorbital, anterior, and cheek lines, and a single midline crossing the nape. Various degrees of development are also present in species of *Ophichthus*, *Echelus*, *Pisodonophis*, *Quassiremus*, *Cirrhimuraena*, *Echiophis*, *Mystrionophis*, and *Aplatophis*. The neuromasts appear as minute papillae and are often difficult to discern due to skin rugosity and a waxy precipitate that forms on preserved specimens.

Neuromast development is probably related to the soft bottom habitat occupied by these species. Schwartz and Hasler (1966) suggested that LL pore development of the mudminnow *Umbra limi* is reduced and free neuromasts are developed in response to its habit of digging into soft mud substrate. In doing so, they suggested, the pores of the LL canal could become impacted with mud and severely impaired. The numerous and widely distributed superficial organs, however would remain functional. Rosenblatt and Rubinoff (1972: 362) inferred a similar adaptation in a heterenchelyid eel in noting that "... the absence of lateral-line pores in *P. asodes* indicate that it may be a burrower in soft mud or in the semiliquid mud-water interface." This inverse relation between sensory neuromasts and LL canal development is further evidenced by the ophichthids in that (a) a general correlation exists between neuromast development and a mud, rather than a sand, substrate occupied by the species involved, (b) free neuromast development is absent in the Sphagebranchini where cephalic pore development is greatest, and (c) conversely, the mud-dwelling species of *Echelus* display extreme pore reduction and moderate neuromast development.

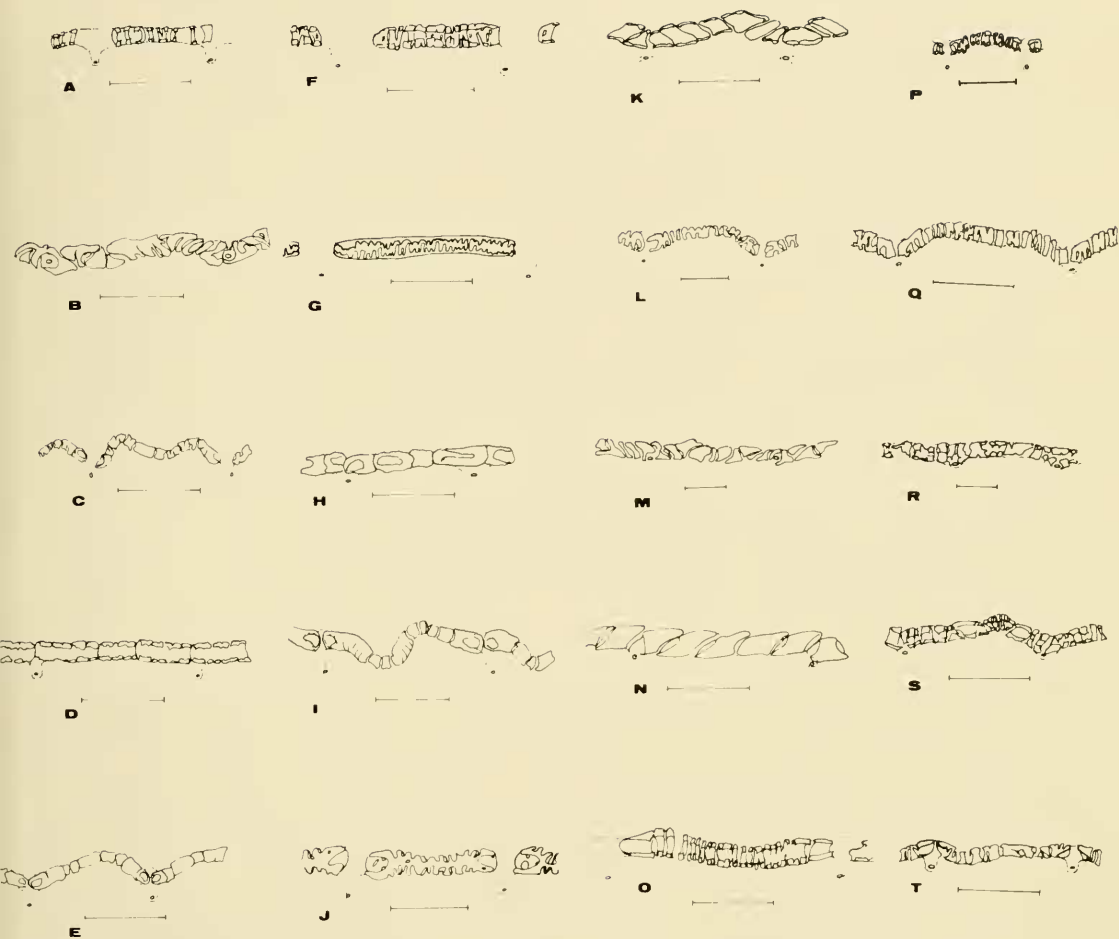


Figure 22. Lateral line ossicles of representative ophichthines. Distal view, right side of mid-trunk region. Scales represent 1 mm. Stippling indicates lateral line canal.

- |                                      |                                    |
|--------------------------------------|------------------------------------|
| A. <i>Aplatophis chauliodus</i>      | K. <i>Phaenomonas pinnata</i>      |
| B. <i>Quassiremus nothochir</i>      | L. <i>Ethadophis byrnei</i>        |
| C. <i>Phyllophichthus xenodontus</i> | M. <i>Ichthyapus selachops</i>     |
| D. <i>Aprognathodon platyventris</i> | N. <i>Yirkala tenuis</i>           |
| E. <i>Myrichthys xystrurus</i>       | O. <i>Caralophia loxochila</i>     |
| F. <i>Ophichthus zophochir</i>       | P. <i>Bascanichthys panamensis</i> |
| G. <i>Cirrhimuraena taeniopterus</i> | Q. <i>Allips concolor</i>          |
| H. <i>Paraetharchus pacificus</i>    | R. <i>Cirricaecula johnsoni</i>    |
| I. <i>Callochelys eristigmus</i>     | S. <i>Lamnostoma orientalis</i>    |
| J. <i>Pisodonophis cancrivorus</i>   | T. <i>Elapsopsis cyclothinus</i>   |

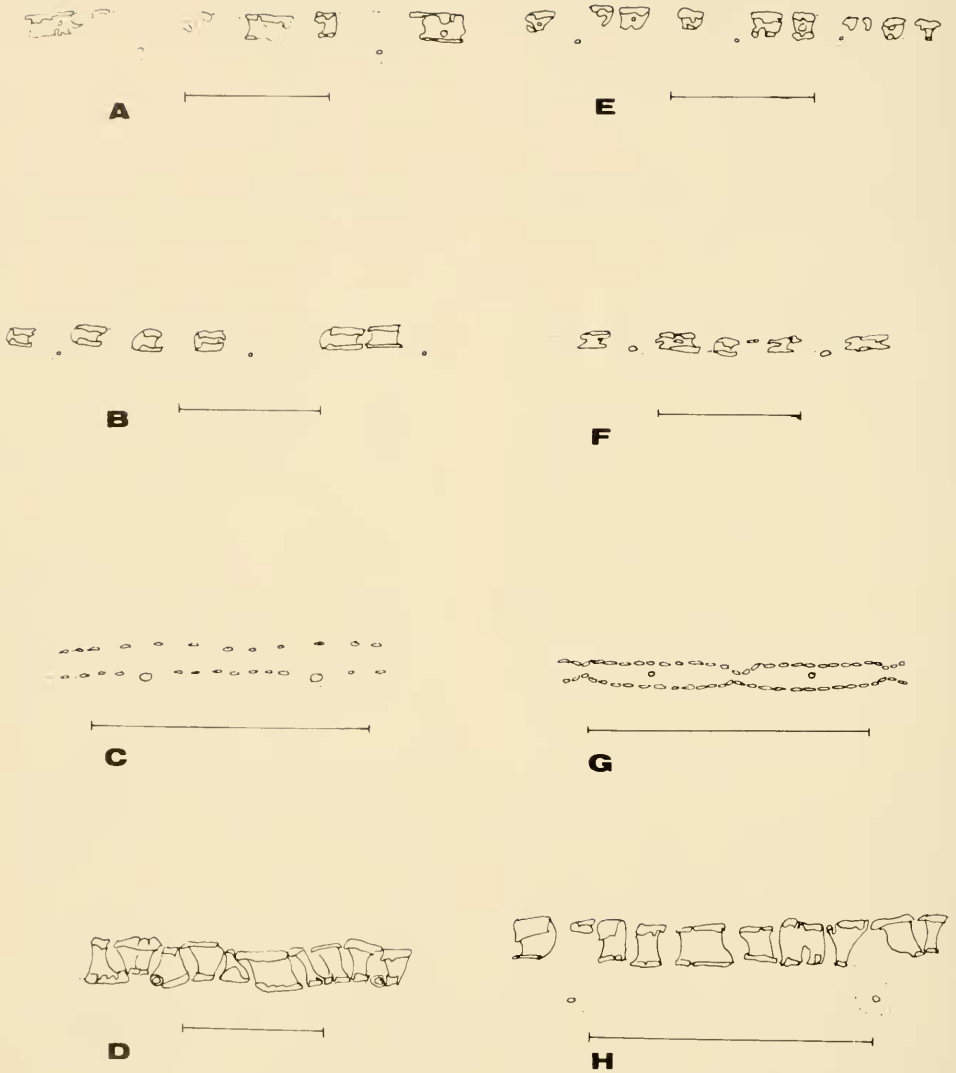


Figure 23. Lateral line ossicles of representative myrophines. Distal view, right side of mid-trunk region. Scales indicate 1 mm. Stippling indicates lateral line canal.

A. *Pseudomyrophis nimius*

B. *Myrophis vafer*

C. *Benthenchelys cartieri*

D. *Muraenichthys chilensis*

E. *Pseudomyrophis micropinna*

F. *Ahlia egmontis*

G. *Schismorhynchus labialis*

H. *Schultzidia johnstonensis*



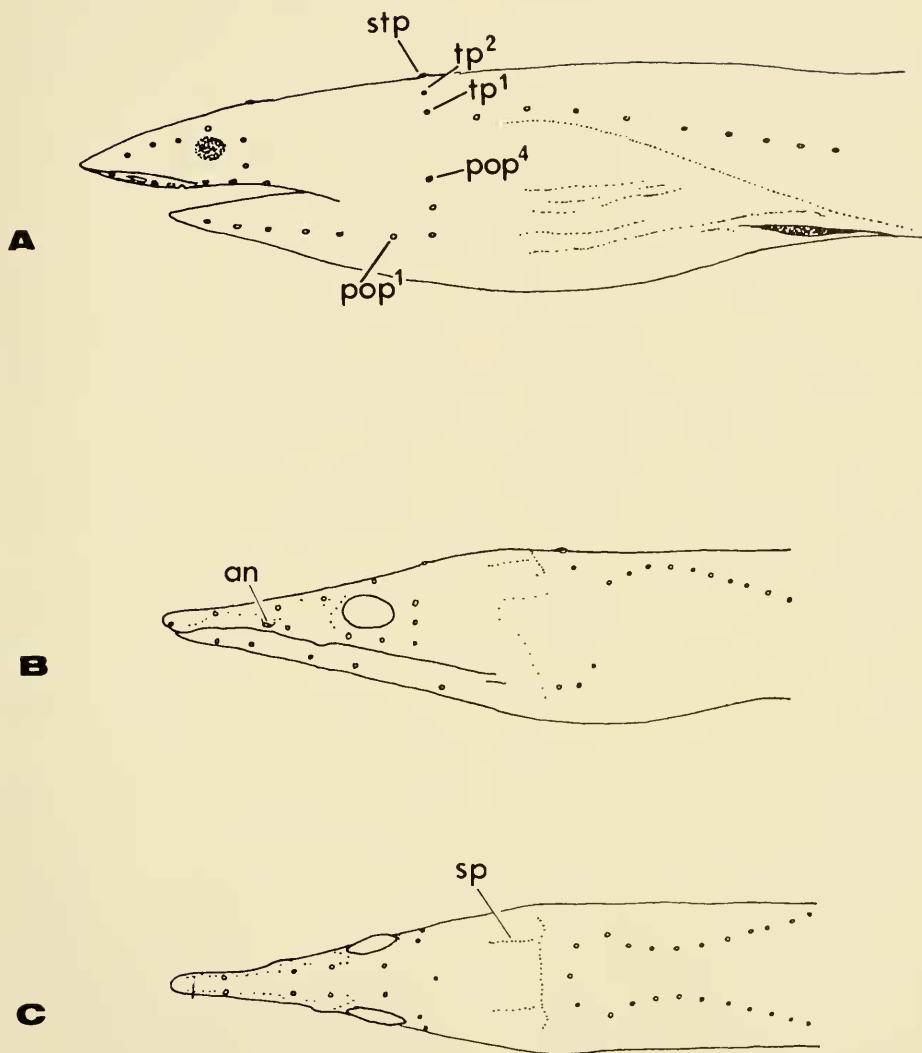


Figure 24. Cephalic pore and surface sensory papillae development in two ophichthids. Abbreviations are: an, anterior nostril; pop<sup>1</sup>, first preopercular pore; sp, surface sensory papillae (free neuromasts); stp, supratemporal pore; tp<sup>1</sup>, first temporal pore.

A. *Ichthyapus selachops*, SIO 65-290. Dotted lines represent contours, not surface sensory papillae.

B. *Ophisurus serpens*, unnumbered Rhodes University specimen, adapted from Allis (1903), left lateral view.

C. *Ophisurus serpens*, dorsal view.

Papillae also occur on the snout and tail tip of several ophichthids (cf. Rosenblatt and McCosker, 1970). Their function has neither been examined nor proposed, but might be inferred from observations and analogous structures on other fishes. Tail tip papillae are generally small and may function as contact sensory devices in relation to the tail-first digging behavior of most observed ophichthids. Certain of the snout papillae are often larger (e.g., in *Leuropharus lasiops* and *Evips percinctus*) and may serve a gustatory as well as a contact sensory function. These papillae are best developed on snouts of several of the small-eyed permanent burrowing species (including species of *Phaenomonas*, *Bascanichthys*, and *Ichthyapus*). A gustatory function for similar papillae on the snout of a heterenchelid eel might also be inferred from Rosenblatt and Rubinoff's (1972: 362) description of *Pythonichthys asodes*. They observed a reduction in the olfactory epithelium and the development of papillae on the jaws of this small-eyed species, and suggested this was related to a fossorial habit. Most species of ophichthids have not reduced their olfactory epithelium, but probably encounter environmental problems similar to those faced by *Pythonichthys* in their modes of feeding.

#### Axial Skeleton

Regan (1912) considered the axial skeleton to be of major importance in separating eel families. He separated the Echelidae (considered by Regan to include *Echelus*, *Ahlia*, *Myrophis*, *Paramyru*, *Chilorhinus*, *Muraenichthys*, and *Eomyru*+) and the Ophichthidae from the Congridae on the basis of the formers' vestigial neural spines. He further separated the Echelidae from the Ophichthidae on the basis of the weaker ribs of the latter family. Gosline (1951a: 302-303) clarified Regan's statements in his discussion of the ophichthid axial skeleton. Difficulties in the preparation and dissection of the anterior vertebrae have precluded their usage in this study in a systematically comparative manner.

The following description is based on the axial skeleton of *Ophichthus zophochir* (figs. 25-26). The first vertebral (V) centrum (CE) is reduced and not fused to the skull (fig. 25A). Its neural arch (NA) extends posteriorly over the second V. A lateral flange on the CE is present on the second and following trunk vertebrae. The NA of V 1-5 are smooth. Along the midline of the NA of V 1-12 is a single longitudinal crest which

is split at its posterior margin to form two short ridges (fig. 26A). Neural spines (NS) are undeveloped on the trunk vertebrae but become weakly developed points posterior to the 6th or 7th caudal vertebra. Epineurals (EN), epipleurals (EP), and pleural ribs (PL) extend posteriorly from the NA and parapophyses (P), and are approximately 5-7 V in length. The EN and EP of most ophichthids begin at the posterior margin of the neurocranium. The P of V 1-12 are posteriorly directed and increase gradually in length. At approximately V 13 the P are symmetrical and shaped like normal isosceles triangles. Foramina exist on each P, slightly posterior to mid-centrum (fig. 26B). The P of V 13-45 (approximate) are homogenous in size and shape; the lateral processes of the following 5-6 V are reduced. The first caudal vertebra (at which point the haemal arch begins to form) differs markedly in having its P split, the upper portion directed laterally to become the first caudal transverse process (CTP) and the lower directed downward to become the haemal arch (figs. 26C-D). The CTP are sharp lateral projections, incised at their midlines to the centrum, and continuing nearly to the caudal tip. The haemal arch closure occurs at approximately the 10th caudal V. The closure however, is incomplete, and consists of the joining of the posterior ends of the haemal spines. Intramuscular (IM) bones replace the neural and pleural ribs in the caudal region.

Differences in neural arch shape and sculpturing are evident in comparing the anteriormost five vertebrae of species of the type genus of each ophichthid tribe (fig. 25). The NA of V 1-5 of members of the Callechelyini can be distinguished, at the tribal level, on that basis alone. Other characters from the axial skeleton were found to be useful indicators of relationship. The parapophyses of certain sphagebranchin genera, for example, were found to possess a marginal process which was lacking in related genera (fig. 33). Also, the CTP are lacking in most myrophins, yet in *Muraenichthys* and related genera the anterior half of the column is similar to the ophichthine column. Finally, the characteristics of the pleural ribs of *Ahlia* and *Myrophis* were found to differ from that of all other ophichthids in that they are limited to the anterior 15-20 vertebrae (see Remarks concerning *Ahlia* and *Myrophis*).

Vertebral numbers have been shown to be useful characters for the separation of species and populations of apodal fishes. Their application to the separation of genera is somewhat difficult because of the high degree of overlap

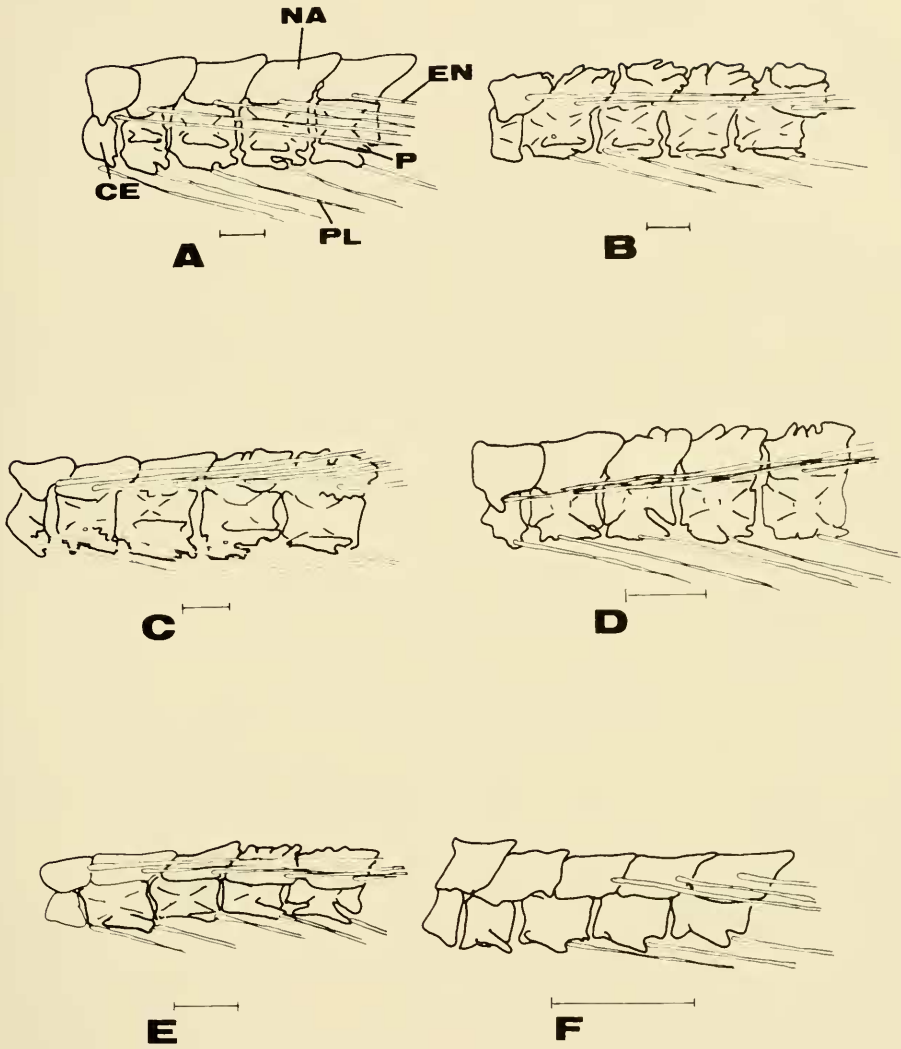


Figure 25. Anteriormost five vertebrae of representative species from the tribes of ophichthids. All are shown in left lateral view. Scale represents 1 mm. Abbreviations are: Ce, centrum; EN, epineural; NA, neural arch; P, parapophysis; PL, pleural rib.

- A. *Ophichthus zophochir*
- B. *Stictorhinus potamius*
- C. *Bascanichthys panamensis*

- D. *Callechelys marmoratus*
- E. *Myrophis vafer*
- F. *Benthenchelys cartieri*

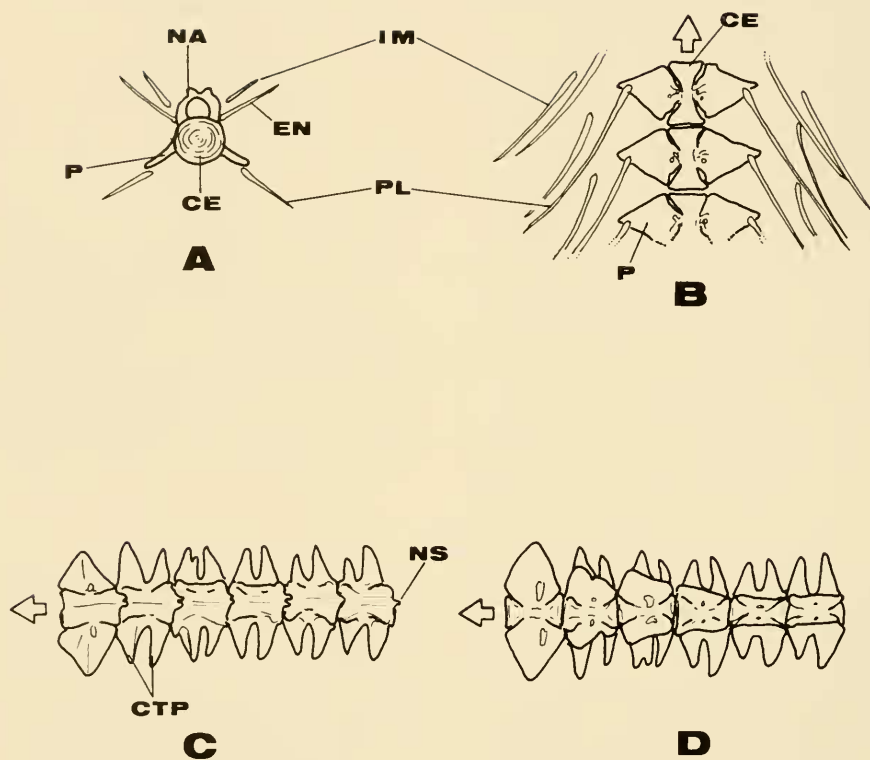


Figure 26. Trunk and caudal vertebrae of *Ophichthus zophochir*. Arrows point anteriorly. Abbreviations are: Ce, centrum; CTP, transverse processes of caudal vertebrae; EN, epineural; IM, intramuscular bone; NA, neural arch; NS, neural spine; P, parapophysis; PL, pleural rib.

- A. Anterior view of 14th vertebra. Ribs appear foreshortened due to viewing aspect.
- B. Ventral view of 14th-16th vertebrae.
- C. Dorsal view of last precaudal (51st) and anterior five caudal (52nd-56th). Ribs and IM bones not illustrated.
- D. Ventral view of vertebrae illustrated in C. Ribs and IM bones not illustrated.

between genera, and a single mean value cannot be applied to a genus. Trends, however, are present within genera, and are probably relatable to the mode of life and associated anatomical specializations of the species involved. The species of *Phaenomonas*, *Allips*, and *Bascanichthys*, for example, tend to have increased vertebral numbers, primarily in the trunk region. An examination of radiographs and gut contents of specimens of those genera disclosed the presence of copious sand and gravel particles in the gut and intestine, and the absence of any recognizable macroscopic animal material. On that basis as well as my observations of live specimens, I suggest that these eels indiscriminately eat their way through the substrate, digesting any utilizable organic material they encounter. In many ophichthids the length of the gut is increased by a loop that extends into the tail portion. The gut of species of *Phaenomonas* and *Bascanichthys* is straight, presumably to prevent blockage by sand particles passing through the lower tract. The increased trunk length, which is typical of these genera, perhaps reflects this problem, and may have been necessary to achieve this feeding mode. Certain callechelyins exhibit a similar increase in trunk vertebrae and a comparable life style.

Vertebral number is also the basis of correlating the pelagic leptocephalus with the transformed adult stage of each eel species. Included in table 6 are the vertebral numbers of eel species examined and radiographed in the course of this study as well as several literature records which are assumed to be correct in species identification. The literature concerning numbers of eel vertebrae has not been exhaustively searched in that errors may inadvertently have been introduced through improper identification.

#### Caudal Skeleton

Differences in the myrophine and ophichthine caudal fins seemed important enough to most earlier authors to recognize the lineages as distinct families. The Ophichthidae of nineteenth century authors was indeed a unique and unified assemblage; primarily due to the conspicuously pointed tail tip. Important members, most notably the species of *Echelus*, were erroneously excluded from the Ophichthidae because they possessed a weakly developed caudal fin. Gosline (1951a: 303) noted the similarity in the ophichthine and myrophine caudal skeletons, but felt that the continuous median fin condition

merited subfamilial separation. His findings, to my knowledge, have not been questioned by subsequent authors. He stated that:

osteologically, the difference between the tails of *Muraenichthys* and *Cirrhimuraena* is less than that between those of *Cirrhimuraena* and *Caecula platyrhyncha*. Rudimentary rays are present around the tails of both *Muraenichthys* and *Cirrhimuraena*; they are embedded in flesh in *Cirrhimuraena* (as also in *Myrichthys*). In *Caecula platyrhyncha*, on the other hand, there are no rudimentary rays either around the tip of the tail or elsewhere. It is obvious from this discussion . . . that a separate family cannot be maintained for *Muraenichthys* on the basis of tail structure.

The findings of this study are in agreement with Gosline's. Difficulties in the dissection and preparation of the caudal skeleton has precluded its wide usage in this study. Careful examination of certain species however (including *Echelus myrus*, *E. pachyrhynchus*, *Leptenchelys vermiformis*, and *Bascanichthys tenuis*), has clarified their position within the family.

The homologies of ossified elements within the apodal caudal skeleton are difficult to determine, and especially so in the case of the sharp-tailed ophichthins and sphagebranchins that have undergone major modification as an adaptation to rapid burrowing. The caudal tip of *Ophichthus zophochir* (fig. 27) is pointed, hard, and without visible caudal rays. The median fins submerge shortly (approximately one eye diameter) before the caudal tip. The underlying osteology is complex, as is illustrated in Figure 27. According to the terminology of Rosenblatt (1967), which was adapted from Nybelin (1963), there is but one weak centrum (CE). Fused to the CE is a pointed hypural (HY) and a much reduced neural arch (NA). Reduced caudal rays (CR) which lack basal elements are imbedded in the skin and weakly associated with the HY. The caudal skeleton of *Myrophis vafer* (fig. 28) differs somewhat from that of *O. zophochir* in possessing a short CE, two elongate HY, and a short cartilaginous extension posterior to each HY. The caudal rays of *Myrophis* are split anteriorly to receive the hypural plate. This is similar to the condition of caudal rays of xencongriids (Robins and Robins, 1967), but appears to differ from the relatively unspecialized condition of *Anguilla* (Smith and Castle, 1972: fig. 19a). Blache's illustration (1968: figs. 5, 10) of the caudal skeleton of *Echelus* indicates a caudal ray attachment similar to that of *Myrophis*. Present in most apodal

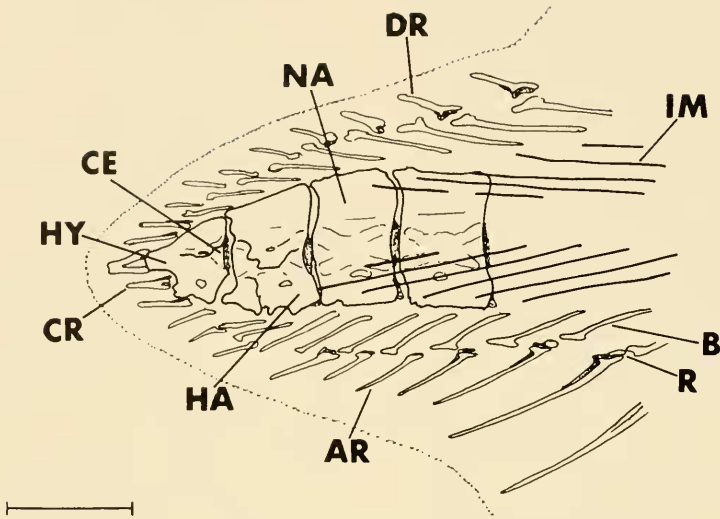


Figure 27. Caudal skeleton of *Ophichthus zophochir*, SIO 65-166. Scale represents 1 mm. Abbreviations are: AR, anal ray; B, basal element of pterygiophore; CE, centrum; CR, caudal ray; DR, dorsal ray; HA, haemal arch; HY, hypural; IM, intramuscular bone; NA, neural arch; R, radial element of pterygiophore.

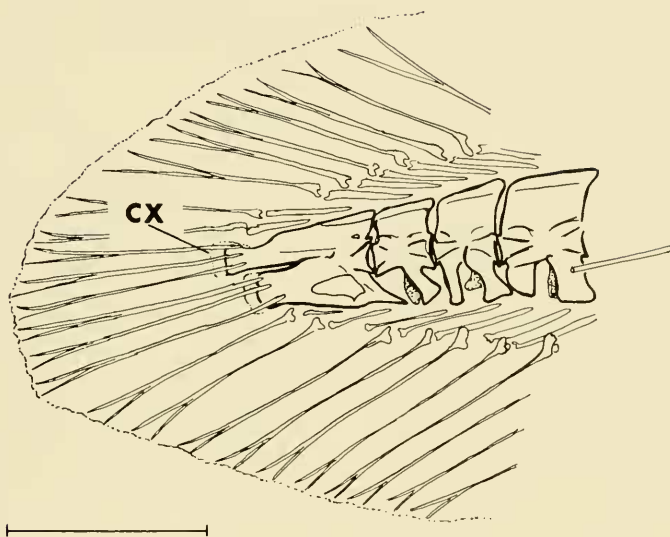


Figure 28. Caudal skeleton of *Myrophis vafer*, SIO 68-242. Scale represents 1 mm. Abbreviation CX is for cartilaginous extension of terminal vertebra.

caudal skeletons is a conspicuous foramen beneath the terminal centrum. It is well-developed in *Myrophis*, but reduced or absent in *Ophichthus* and other ophichthines, resulting from the reduction of the lower HY. The haemal arches (HA) of the posterior caudal vertebrae of *Ophichthus* and other ophichthines differs from that of *Myrophis* and other myrophines. The ophichthine condition appears to be that of a simple rectangular lateral plate, whereas in the myrophines a wide gap separates the HA into an anterior and a posterior lateral flange.

The presence of a myrophin-like caudal fin in species of *Echelus* and *Leptenchelys* requires further explanation. As stated above, rudimentary fin rays are present in the sharp-tailed ophichthines. In the discussion of the evolution of the Ophichthidae it is hypothesized that the elongate bascanichthyins separated early in the evolution of the Ophichthinae, and in general, they possess a blunt rather than extremely sharp pointed tail tip. The tail of *Bascanichthys tenuis* is surrounded by a weak epidermis, which without careful inspection gives the appearance of a rayed caudal fin. The caudal tip of *B. tenuis*, when viewed with transmitted light, was found to lack caudal fin rays. The type and only known specimen of *Leptenchelys vermiformis* is similar to *B. tenuis* in possessing loose epidermis at the caudal tip, although minute fin rays appear to be present. The fin ray development in this juvenile specimen may be anomalous, or may represent a redevelopment of the rudimentary fin rays characteristic of the ancestral condition. The caudal fin of *Echelus myrus*, in contrast to the bascanichthyin fins, has well developed fin rays. The caudal skeletons of *Ophichthus zophochir* and *E. myrus* do not markedly differ other than in the development of fin rays. The produced rays appear to be a primitive retention of an ancestral condition, whereas the hard-pointed tail tip of other ophichthines was developed early in the evolution of the family. Other primitive morphological characters of *Echelus* that bear similarities to the generalized ophichthines and certain congridids would suggest that *Echelus* is a primitive ophichthid not far from the basal ophichthine stock.

The caudal skeletons of several ophichthids have been illustrated by earlier authors. Included are: *Benthenchelys cartieri* (Castle, 1972); *Echelus myrus*, *E. pachyrhynchus*, and *Myrophis plumbus* (Blache, 1968); *Mystriophis rostellatus*, *M. crosnieri*, and *Echiophis intertinctus* (Blache,

1971); *Myrichthys pardalis*, *Bascanichthys* spp., and *Callechelys* spp. (Blache and Cadenat, 1971); and *Muraenichthys cookei* and *Cirrhimuraena macgregori* (Gosline, 1951a).

#### Visceral Anatomy

The digestive tract and gas bladder have been shown by Asano (1962) to be useful taxonomic characters within the Congridae. This study is concerned primarily with osteology and the soft anatomy was therefore not examined in a systematic manner.

A cursory examination of a myrophine, *Myrophis vafer* (SIO 68-286, 240 mm TL), and an ophichthine, *Ophichthus zophochir* (SIO 65-166, 335 mm TL), disclosed very similar digestive tracts and gas bladder morphologies (fig. 29). The digestive tract in both species includes a gut diverticulum, or stomach (fide D. Smith, 1971), which branches off the anterior trunk region and extends posteriorly as a blind sac. The intestine, in both species examined, is a straight tube opening directly into the anus, whereas in other ophichthids it appears to extend partially into the caudal region and then to loop forward to the anus. The gas bladder (GB) connects anteriorly to the intestine through the pneumatic duct (PD) at the mid-trunk level. The GB of both species is thin walled, surrounded by a thin mesentery, and lies alongside the intestine and dorsally within the peritoneal cavity. The GB is white, shiny and flexible; the digestive tract is pale in both species.

The gas bladder of the above-mentioned species occupies little of the peritoneal cavity, as might be expected from their fossorial habits. The GB of the pelagic species *Benthenchelys cartieri* however, is considerably longer than that of either of the two fossorial species (Castle, 1972; fig. 25). Its length is approximately one-third of the trunk length, whereas the other two are approximately one-fourth to two-ninths. The GB of congrid eels is longer than the stomach (cf. Asano, 1962; D. Smith, 1971). The GB of the three ophichthids, by contrast, is considerably shorter than the stomach.

#### TAXONOMY

The following section includes an osteological definition of the family, a dichotomous key for the identification of genera, a diagnosis of the subfamilies and tribes, and an osteological and external morphological description of each genus of the Ophichthidae.



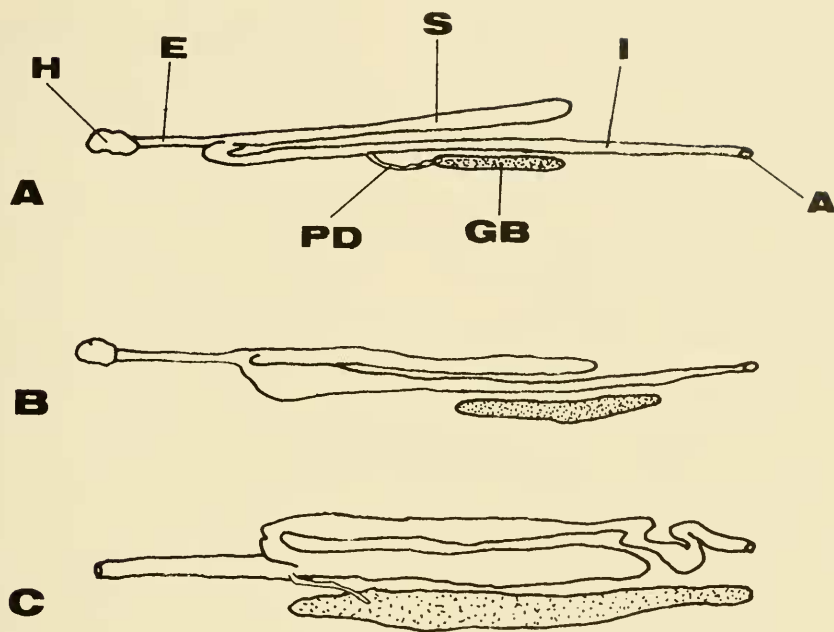


Figure 29. Comparative anatomy of congrid and ophichthid digestive tract and gas bladder. The gas bladder has been separated from the intestine and the mesentery removed to improve clarity. The gas bladder is stippled for identification, not to indicate pigmentation. Not drawn to scale. Abbreviations are: A, anus; E, esophagus; GB, gas bladder; H, heart; I, intestine; PD, pneumatic duct; S, stomach.

- A. *Ophichthus zophochir*, SIO 65-166
- B. *Benthenchelys cartieri*, after Castle (1972)
- C. *Conger myriaster*, after Asano (1962)

The generic key is constructed using both osteological and external morphological characters. An attempt is made to group genera within the key in a natural manner to indicate relationships.

In this section, redundancy is avoided wherever possible, however in several instances important characters are repeated both in the tribal diagnoses and generic descriptions to facilitate comparisons. The generic descriptions are based, whenever possible, on the type species as well as the most morphologically divergent species within each genus, in an attempt to include the range of variation for each character examined. In a few instances the type species of the genus was unavailable for osteological study. Those genera are identified in the remarks section following each description. The included nominal species of each genus are listed under the head-

ing "distribution". Those species known to me only from literature records are indicated by an asterisk (\*).

Abbreviations of several morphological characters and conditions are included for the sake of brevity. The reader is referred to the listing of abbreviations in the Materials and Methods of this paper. Also note that Body = Head + Trunk when used in body and tail length comparisons. The symbol  $\approx$  means "approximately equal to".

#### Osteological Definition of the Ophichthidae

From the present study the following osteological definition of the Ophichthidae may be developed:

- (a) branchiostegal rays numerous and broadly overlapping along the ventral midline;
- (b) supraorbital canals united by a transverse commissure through the fused frontals;
- (c) temporal canal present;

- (d) frontals of adults fused for their entire length and lacking an obvious suture;
- (e) first epibranchial connected by a continuous cartilaginous strap to the second infra-pharyngobranchial;
- (f) no more than first basibranchial ossified;
- (g) third hypobranchial usually cartilaginous;
- (h) neural spines rudimentary or absent;
- (i) tongue adnate;
- (j) palatine absent;
- (k) pterygoid well separated from vomer and generally free from hyomandibular.

*Analytical Key to the Genera of Ophichthidae*

- 1a. Accessory branchiostegal rays originate behind ends of epihyal (EH), free rays more numerous than attached; caudal fin rays conspicuous, confluent with dorsal and anal, tail tip flexible; gill openings (GO) mid-lateral, a constricted opening ..... *Myrophinae* .....2
- 1b. All branchiostegal rays originate either in association with hyoid or before level of EH tips; free rays, when present, fewer than attached; tail tip a hard or fleshy finless point; GO mid-lateral to entirely ventral, un-constricted .....*Ophichthinae*.....9

- 2a. Neurocranium short, pointed anteriorly, broad posteriorly, length/depth  $\leq 3$ ; eye large, ca. 6 times in head, orbital foramen large, its depth ca. 0.5 skull depth; anterior nostril non-tubular; (posterior nostril before eye; pectoral fin moderately developed) .....*Benthenchelyini* .....  
..... *Benthenchelys*
- 2b. Neurocranium more elongate, length/depth  $\geq 4$ ; eye smaller, 10 or more in head, orbital foramen smaller, its depth much less than 0.5 skull depth; anterior nostril tubular ..... *Myrophini* .....3
- 3a. Pleural ribs absent behind 15th-20th trunk vertebra; pectoral fin well developed .....4
- 3b. Pleural ribs present on all trunk vertebrae; pectoral fin either absent or moderately developed .....5
- 4a. Vomerine teeth absent; dorsal fin origin (DFO) above or behind anus; maxilla stout, not tapering posteriorly, and abutting pterygoid (fig. 30A); hypohyals (HH) absent, glossohyal (GH) rudimentary .....*Ahlia*
- 4b. Vomerine teeth present; DFO anterior to mid-trunk region; maxilla thin and tapering posteriorly, not closely associated with pterygoid (fig. 30B); HH separated from

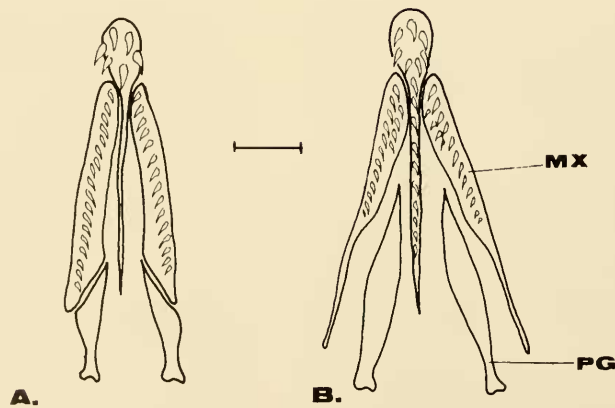


Figure 30. Vomer, maxillae, and pterygoid of *Ahlia egmontis* (A) and *Myrophis vafer* (B). Scale represents 1 mm. Abbreviations are: MX, maxillae; PG, pterygoid.

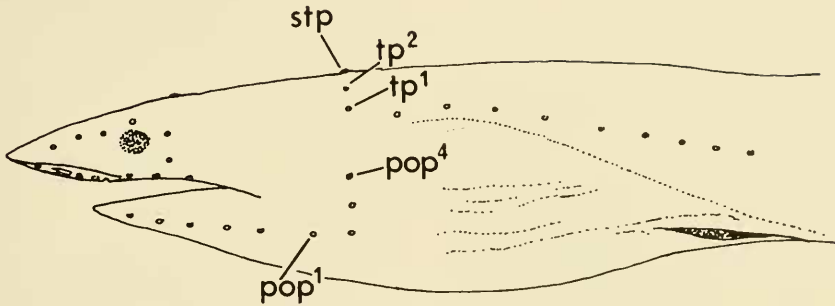


Figure 31. Diagrammatic representation of a species with well developed head pores.

- ceratohyal by a gap, GH normally developed .....*Myrophis*
- 5a. Pectoral fin present, coracoid (Co) and sometimes scapula (Sc) present; posterior nostril lateral; transverse processes of caudal vertebrae (CTP) absent .....6
- 5b. Pectoral fin absent, girdle reduced to cleithrum (Cl) and supracleithrum (SCL); posterior nostril labial; CTP present .....7
- 6a. Pectoral fin minute, Sc and actinosts absent .....*Pseudomyrophis*
- 6b. Pectoral fin well-developed, Sc, Co, and actinosts present .....*Neenchelys*
- 7a. Teeth absent on vomer, absent or embedded on intermaxillary, those on maxilla and dentary minute or villiform; supraoccipital (SO) extends anteriorly to frontals, completely separating parietals; SO crest absent .....*Schultzidia*
- 7b. Teeth present on intermaxillary, maxilla, dentary, and vomer; SO not extending beyond parietals; SO crest present .....8
- 8a. A prominent toothed groove on underside of snout, bordered by dermal folds, extending anteriorly to anterior nostrils; hypohyals (HH) fused to ceratohyals (CH); suspensorium forwardly inclined .....  
..... *Schismorhynchus*
- 8b. Underside of snout without a prominent median toothed groove bordered by dermal folds; HH broadly separated from CH by a suture; suspensorium nearly vertical ..... *Muraenichthys*
- 9a. Neurocranium short, terete, length/depth ca. 3 or less; dorsal fin origin (DFO) on nape, above supraoccipital (SO); head pores reduced pop<sup>3</sup>, pop<sup>4</sup>, and tp<sup>2</sup> absent (fig. 31); hyoid stout, thickened; (gill openings (GO) inferior, parallel or converging forward, isthmus narrower than GO length; pectoral fin absent) .....*Callechelyini* .....10
- 9b. Neurocranium longer, length/depth 4 or more; DFO, if present, behind nape; head pores generally not reduced, may include pop<sup>3</sup>, pop<sup>4</sup>, tp<sup>2</sup>; hyoid more slender .....14
- 10a. Intermaxillary teeth absent; hypohyals (HH) absent; third hypobranchial (H<sub>3</sub>) ossified ..  
..... *Aprognathodon*
- 10b. Intermaxillary teeth present; HH broadly separated from ceratohyal by a suture; H<sub>3</sub> cartilaginous .....11
- 11a. Anterior nostril rim not raised; dorsal fin origin (DFO) above epiotics; neurocranium slightly depressed, not convex across parietal-frontal region; four supraorbital pores; (anal fin absent; snout not grooved) .....  
..... *Letharchus*
- 11b. Anterior nostril tubular; DFO above supraoccipital; neurocranium rounded across parietals and frontals; three supraorbital pores .....12
- 12a. Anal fin absent; gill openings (GO) expanded ventrolaterally, forming broad pockets .....*Paraletarchus*
- 12b. Anal fin present; GO only slightly expanded, not forming broad pockets .....13

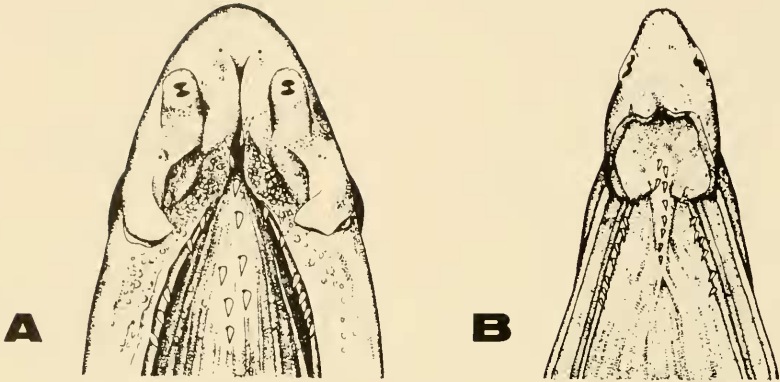


Figure 32. Representation of underside of callechelyin snouts. A. Median groove present (13a in key), as in *Callechelys*. B. Median groove absent, as in *Letharchus*.

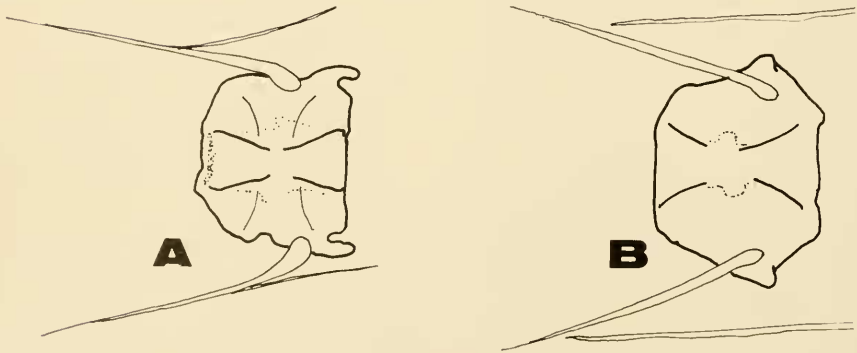


Figure 33. Diagrammatic representation of posterior trunk vertebrae (37th), ventral view. A. Parapophyses with anterior projection (16a in key), as in *Apterichtus*. B. Anterior projection absent (16b in key), as in *Stictorhinus*.

- 13a. Vomer toothed; median groove on underside of snout (fig. 32A); snout and nape not heavily papillate .....*Callochelys*
- 13b. Vomerine shaft toothless; no median groove on underside of snout; snout and nape with numerous papillae ..*Leuropharus*
- 14a. Pectoral fin absent or vestigial; pectoral girdle reduced, consisting of a cleithrum (Cl), and may include a supracleithrum (SCI) and reduced scapula (Sc) and coracoid (Co); median fins reduced or absent ..... 15
- 14b. Pectoral fin present, generally well developed; pectoral girdle consists of Cl, SCI (except in *Scytalichthys*), and generally Sc, Co, and actinosts; median fins generally elevated ..... *Ophichthini* ..... 29
- 15a. Neurocranium depressed and elongate, length/depth  $\geq 4$ ; head pores developed,  $tp^2$  and  $pop^3$  generally present; gill openings (GO) entirely ventral (except in *Yirrkala*) .....*Sphagebranchini* .....16
- 15b. Neurocranium deeper and shorter, length/depth  $\leq 4$ ; head pores reduced,  $tp^2$  and  $pop^3$  absent; GO low lateral, crescentic ....*Bascanichthyini* .....22
- 16a. All fins absent; parapophyses of posterior trunk vertebrae with an anterior marginal projection (fig. 33a); pectoral girdle reduced to a cleithrum and a reduced or absent supracleithrum; branchiostegal rays few, generally fewer than 20 pairs; second basibranchial ( $B_2$ ) absent .....17
- 16b. Median fins present; anterior margin of posterior trunk vertebral parapophyses entire (fig. 33b); pectoral girdle includes cleithrum, supracleithrum, and reduced scapula and coracoid; branchiostegal rays more numerous, more than 20 pairs;  $B_2$  cartilaginous .....19
- 17a. Upper pharyngeal tooth plates ( $UP_3$  and  $UP_4$ ) fused; cirri present on upper lip .....*Cirriacaecula*
- 17b.  $UP_3$  and  $UP_4$  separate; upper lip smooth.... 18
- 18a. Posterior nostril opening outside mouth, with a flap; anterior nostril tubular; eye moderately developed .....*Apterichthys*
- 18b. Posterior nostril opening inside mouth, with or without a flap; anterior nostril flush with snout; eye minute .....*Ichthyapus*
- 19a. Lateral head profile, from above, narrows sharply from epiotics to interorbital, then extends evenly to a pointed snout; body stout, its depth less than 30 in its length; vomerine teeth enlarged, pointed and recurved ..... *Lamnostoma*
- 19b. Lateral head profile narrows evenly from epiotics to snout; body moderately elongate, its depth more than 40 in its length; vomerine teeth conical, not enlarged ....20
- 20a. Eye minute,  $\geq 5$  in snout; anterior nostril flush along snout; interopercle (IOP) absent ..... *Stictorhinus*
- 20b. Eye larger,  $\leq 3$  in snout; anterior nostril tubular, or with a short but noticeable rim; IOP present .....21
- 21a. Neurocranium nearly flat across parietals and epiotics; gill openings (GO) with an anterolateral duplication forming a pouch; accessory branchiostegals loosely attached to hyoid, fewer than half associated with epihyal (EH); interopercle (IOP) subrectangular, margin entire .....*Caecula*
- 21b. Neurocranium raised along dorsal midline, not broad and flat across parietals and epiotics; gill membrane without a duplication; accessory branchiostegals closely associated with hyoid, more than half associated with EH; IOP rounder, serrated along margin .....*Yirrkala*
- 22a. Tail short, .300-.360 of total length (TL); body extremely elongate, its depth ca. 75-160 times in TL .....23
- 22b. Tail longer, .395-.530 of TL; body not extremely elongate, its depth usually less than 70 in TL .....24
- 23a. Dorsal fin originating just behind occiput and ending less than 2 head lengths behind gill openings; anal fin lacking .....*Phaenomonas*
- 23b. Vertical fins low, but extending nearly to tail tip .....*Gordiichthys*
- 24a. Pectoral fin absent; supraoccipital crest (SOC) extends from a parietal ridge, becoming a raised point posteriorly .....25
- 24b. Pectoral fin a minute flap in upper gill opening corner; SOC nearly rounded, little or no posterior point .....28
- 25a. Dorsal fin origin (DFO) behind gill openings (GO); tail longer than body; gill arches stout, third hypobranchial ( $H_3$ ) ossified, fifth ceratobranchial ( $C_5$ ) a slender ossified rod .....*Dalophis*
- 25b. DFO above or behind GO; body  $\geq$  tail; gill arches reduced,  $H_3$  cartilaginous,  $C_5$  absent .....26

- 26a. Anterior nostril not tubular, its rim not raised, developed as an opening with lateral projections into it; underside of snout not grooved; intermaxillary teeth inconspicuous ..... *Caralophia*
- 26b. Anterior nostril tubular; underside of snout grooved; intermaxillary teeth conspicuous ..... 27
- 27a. Median fins continuous around caudal, caudal fin rays evident ..... *Leptenchelys*
- 27b. Caudal tip blunt, finless ..... *Ethadophis*
- 28a. Dorsal fin origin on head ..... *Bascanichthys*
- 28b. Dorsal fin origin more than a head length behind head ..... *Allips*
- 29a. Fifth ceratobranchial ( $C_5$ ) absent ..... 30
- 29b.  $C_5$  present as a slender rod, either ossified or cartilaginous ..... 34
- 30a. Third preopercular pore ( $pop^3$ ) present; pectoral fin rudimentary, smaller than eye; pectoral girdle reduced to cleithrum and supracleithrum ..... *Quassiremus*
- 30b.  $pop^3$  absent; pectoral fin well developed, longer than eye; scapula and coracoid of pectoral girdle present ..... 31
- 31a. Hypohyals (HH) absent; maxilla with a forward projection, articulated ca. mid-vomer; supraoccipital (SO) rounded, lacking a posterior projection; urohyal (UH) deeply notched anteriorly; anterior nostrils with conspicuous leaflike appendages ..... *Phyllophichthus*
- 31b. HH present, separated from ceratohyal by a suture; maxilla without anterior projections, articulated before mid-vomer; SO with a posterior projection; UH not notched beyond midpoint of basal plate; anterior nostrils without leaflike appendages ..... 32
- 32a. Jaws subequal; upper pharyngeal tooth plates ( $UP_3$ - $UP_4$ ) separate ..... *Pogonophis*
- 32b. Lower jaw inferior;  $UP_3$ - $UP_4$  fused ..... 33
- 33a. Third hypobranchial ( $H_3$ ) ossified; actinosts present; vomerine teeth present ..... *Elapsopis*
- 33b.  $H_3$  cartilaginous; actinosts absent; vomerines absent, or 1-3 small teeth ..... *Leiuranus*
- 34a. Teeth molariform or granular; pectoral fin broad-based (fig. 34A) ..... 35
- 34b. Teeth pointed; pectoral fin base restricted, opposite upper half of gill openings (fig. 34B) ..... 36
- 35a. Dorsal fin origin above or behind gill openings (GO); third preopercular pore ( $pop^3$ ) usually present; hypohyals (HH) narrowly separated from ceratohyal (CH); supraoccipital (SO) with a posterior projection ..... *Pisodonophis*
- 35b. DFO well in advance of GO;  $pop^3$  absent; HH broadly separated from CH; SO rounded, without a posterior projection.... *Myrichthys*
- 36a. Eye before middle of upper jaw, preorbital portion of neurocranium not extending beyond posterior 2/3, rostral portion of ethmoid shorter than orbit; some teeth long and fanglike ..... 37
- 36b. Eye over middle of upper jaw, preorbital portion of neurocranium extends nearly to or beyond middle of skull; rostral portion of ethmoid about equal in length to orbit; teeth not fanglike ..... 42
- 37a. Lower jaw projects considerably; anterior teeth of both jaws long fanglike canines extending far outside mouth; frontal crest a conspicuous sharp ridge ..... *Aplatophis*
- 37b. Lower jaw inferior or jaws nearly subequal; anterior teeth in jaws not fangs extending beyond snout tip; frontals not forming a sharp ridge, neurocranium rounded or flat dorsally ..... 38
- 38a. Tail longer than body, compressed posteriorly; pectoral developed, 5 or less in head length; third preopercular pore ( $pop^3$ ) present ..... 39
- 38b. Tail shorter than or nearly equal to body; pectoral reduced, 7 or more in head length;  $pop^3$  absent ..... 40
- 39a. Snout short, 7-12 in head length; secondary cephalic papillae absent ..... *Echiophis*
- 39b. Snout longer, 6 or less in head length; secondary cephalic papillae well developed ..... *Mystriophis*
- 40a. Postorbitals strongly developed, forming a postorbital strut; branchiostegals fewer than 20; postorbital region with a conspicuous transverse depression; lips fringed; coloration uniform ..... *Brachysomophis*
- 40b. Postorbitals moderately developed, not forming a strut; branchiostegals 20 or more; dorsolateral profile of head even; lips entire; body spotted ..... 41
- 41a. Pectoral fin minute, more than 8 in head length; body much longer than tail ..... *Scyalichthys*
- 41b. Pectoral fin better developed, ca. 7 in head length; body and tail nearly subequal ..... *Xyrias*
- 42a. Pectoral fin rudimentary,  $\cong$  eye; body longer than tail; (third preopercular pore

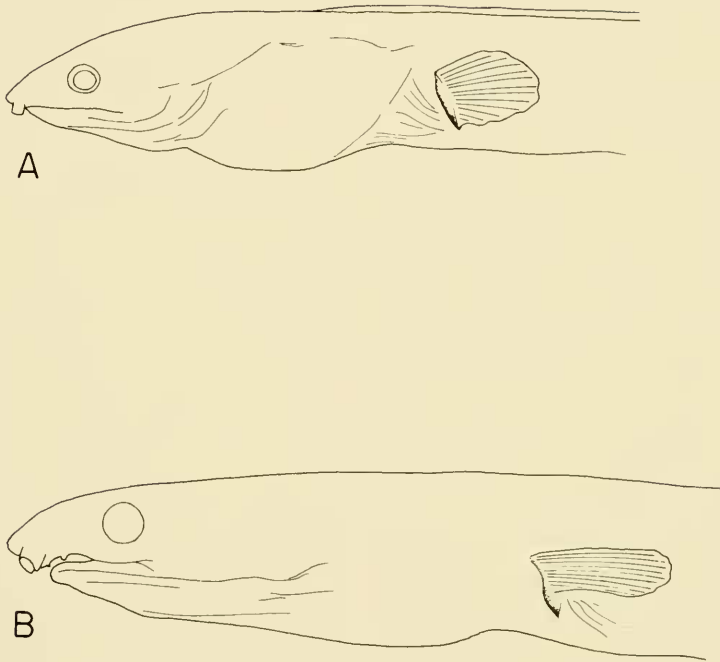


Figure 34. Diagrammatic representation of head and pectoral fin of two ophichthins. A. Pectorals broad-based (34a in key), as in *Myrichthys*. B. Pectoral base restricted (34b in key), as in *Ophichthus*.

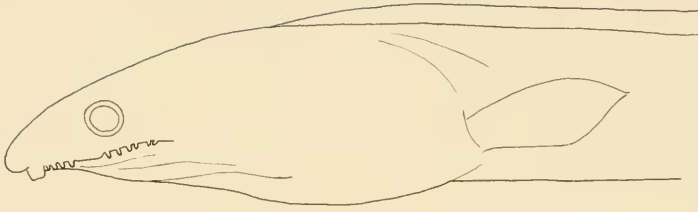


Figure 35. Diagrammatic representation of an ophichthin with a fringed upper lip (46b in key).

- absent) .....*Evips*
- 42b. Pectoral fin developed, noticeably longer than eye; tail longer than body .....43
- 43a. Caudal fin present, confluent with dorsal and anal; temporal, postorbital, and interorbital pores absent .....*Echelus*
- 43b. Tip of tail a finless point; temporal, postorbital, and interorbital pores present ....44
- 44a. Dorsal fin origin (DFO) before gill openings (GO); third preopercular pore ( $pop^3$ ) absent; upper pharyngeal tooth plates ( $UP_3$ - $UP_4$ ) fused; pectoral girdle reduced, scapula (Sc), coracoid (Co), and actinosts absent .....*Malvoliophis*
- 44b. DFO behind GO, or if before, the upper lip is fringed;  $pop^3$  usually present;  $UP_3$ - $UP_4$  separate; Sc, Co, and actinosts present ..... 45
- 45a. Snout very long, attenuate, ethmoid/neurocranium  $\geq .500$ ; jaws slender and elongate, incapable of closing completely in adults ..  
..... *Ophisurus*
- 45b. Snout moderate or short, ethmoid/neurocranium  $< .500$  jaws not slender and elongate, capable of closing completely..46
- 46a. Upper lip not fringed, although a barbel may be present; dorsal fin origin (DFO) behind gill openings (GO); opercular series stout, not weak and serrated along margin; actinosts usually 3-4 .....*Ophichthus*
- 46b. Upper lip fringed (fig. 35); DFO generally on head, or above GO; opercular series weak, subopercle reduced; actinosts 1-2....  
..... *Cirrhimuraena*

#### Kaup's Genera

Kaup published his generic and specific descriptions twice in 1856. The earlier treatment, "Ubersicht der Aale" (1856a), is mentioned by John Edward Gray in the preface of the second, the *Catalogue of Apodal fish in the Collection of the British Museum* (1856b), published on 30 December 1856. Gray stated that "During the printing of the work and the engraving of the plates . . . a synopsis of the genera and new species has been published by Dr. Kaup, in German, in the *Archiv. fur Naturgeschichte*, xxii. 41, 1856." Kaup altered several generic names in the latter work (*Echiophis* became *Echiopsis*, *Ophisurapus* - *Ophisuraphis*, and *Pisodonophis* - *Pisoodonophis*), which has resulted in variant spellings of these generic names. Bleeker (1865) emended the spelling of several of Kaup's genera, but Jordan (1919b) returned to Kaup's earlier work. In the following listings of generic synonymies, the pagination of Kaup's later work (1856b) will follow that of the earlier, set off in parentheses.

Type species were not designated by Kaup for his numerous and short-lived genera. Bleeker (1865), as first reviser, synonymized most of Kaup's genera before types were designated. Jordan seems to have been the first to designate types for Kaup's invalid genera, and it appears that in each case the first species listed by Kaup was regarded as the type species (cf. Jordan, 1922).

#### Subfamilial and Tribal Diagnoses and Generic Descriptions



## Subfamily Myrophinae

DIAGNOSIS: GO mid-lateral, a constricted opening; DFO behind mid-trunk; caudal fin rays not reduced, externally visible, confluent with dorsal and anal, tail tip flexible; nasals cartilaginous or absent; ceratohyal not divided into a short median and a long distal portion (fig. 17B); only basal plate of urohyal ossified, posterior extension cartilaginous; accessory branchiostegal rays originate behind tips of epihyal, free rays more numerous than attached; branchial skeleton reduced, basibranchials generally limited to first, fifth ceratobranchial absent; coloration uniform or darkened dorsally.

## Tribe Benthenchelyini

TYPE GENUS: *Benthenchelys* Fowler, 1934

DIAGNOSIS: Body moderately elongate, laterally compressed behind head; tail much longer than body; anterior nostril not tubular, posterior nostril lateral, before center of orbit; GO lateral, a horizontal ellipse; median fins elevated; pectoral fin moderately developed; head pores enlarged, a single preopercular pore, frontal commissure weakly developed; LL ossicles fragmentary, nearly absent; neurocranium short, rounded (fig. 4); otic bulla, nasals, and SOC absent; maxilla broad, not produced posteriorly (fig. 16), articulating beneath anterior margin of orbit; gill arches weakly ossified, B<sub>1</sub> cartilaginous, H<sub>3</sub> ossified, UP<sub>3</sub>-UP<sub>4</sub> fused; pectoral girdle moderately developed, SCI, CI, Sc, and Co present; IM bones and ribs weakly developed, CTP absent; epipleurals limited to anterior 14-16 vertebrae; vertebrae distinctive (fig. 25), neural arches prominent; caudal more numerous than precaudal vertebrae; coloration uniform, slightly darker dorsally. Other characters those of the single genus.

REMARKS: *Benthenchelys cartieri* was described by Fowler (1934) and referred to the Derichthyidae (also Beebe, 1935). Gosline (1952) referred it to the Congridae. Subsequently, Castle (1972) has recognized it as an ophichthid after a thorough osteological study. The distinctness of this monotypic genus is herein felt to merit tribal recognition. The Benthenchelyini appear to be a distinctive offshoot from the generalized Myrophini, specialized for a pelagic mode of life. Specializations include the large eye, compressed body, enlarged median fins, enlarged head pores, and slender dentition. These characteristics converge with those of other pelagic eels, especially

the genus *Derichthys*. A myrophin relationship, particularly to the generalized *Myrophis*, is evidenced in the hyoid and branchial arches, gill opening, frontal commissure, and disappearance of the epipleural ribs. The pelagic life style of *Benthenchelys* (and the associated eye enlargement), unique to the Ophichthidae, could have evolved from the epipelagic breeding migrations of certain myrophines (see Cohen and Dean, 1970).

*Benthenchelys* Fowler

*Benthenchelys* Fowler 1934: 267. (Type species; *B. cartieri* Fowler 1934, by original designation.)

DESCRIPTION (supplementing tribal diagnosis): snout blunt; jaws nearly subequal; eye large; anterior nostril not tubular, a large antieriad opening; DFO slightly before vent; jaw and vomerine teeth conical, recurved, and uniserial, intermaxillary teeth flattened and directed anteriorly, separated from those of vomer by a gap; nasal cartilage weakly developed; suspensorium anteriorly inclined, jaw angle ca. 95°; maxilla broad, not produced posteriorly, articulating beneath anterior margin of orbit; hyoid weak, GH elongate, HH separated from CH by a gap, UH a subrectangular plate anteriorly, a cartilaginous filament posteriorly; branchiostegal rays numerous, 8 along EH, the last 2 joined basally.

ETYMOLOGY: From the Greek βένθος (benthos), deep, and ἐνχέλυσ (enchelys; either masculine or feminine, here to be treated as masculine), eel.

DISTRIBUTION: A single pelagic species (100-250 meters) over deep water in the central Indo-Pacific.

## Tribe Myrophini

TYPE GENUS: *Myrophis* Lütken, 1851

DIAGNOSIS: Body short to extremely elongate, laterally compressed behind head; tail generally longer than body; lower jaw included; anterior nostril tubular; posterior nostril either lateral or labial; GO lateral, a constricted opening; median fins low or elevated, DFO behind mid-trunk; pectoral fin present or absent; head pores variably developed; LL canal weakly ossified; intermaxillary dentition and vomerine, when present, continuous; neurocranium not raised along frontal or parietal midline, SO crest developed in

some genera; orbit moderately developed; gill arches reduced, weakly ossified, B<sub>1</sub> often absent, B<sub>2-4</sub> absent or rudimentary; pectoral girdle development variable; IM bones and ribs moderately to weakly developed, transverse processes of caudal vertebrae present in some genera; epipleurals limited to anterior trunk vertebrae in some genera; caudal vertebrae more numerous than precaudal; coloration uniform, often darker dorsally.

*Ahlia* Jordan and Davis

*Ahlia* Jordan and Davis 1891: 639. (Type species; *Myrophis egmontis* Jordan 1889, by original designation.)

DESCRIPTION: General characters those of *Myrophis*. Differences include: snout sub-conical, broad; DFO above or behind anus; vomerine teeth absent; maxilla broad, not tapering posteriorly, closely abuts the short and broad pterygoid (fig. 30); HH absent, GH rudimentary; gill arches reduced, H<sub>3</sub> and I<sub>2</sub> absent.

ETYMOLOGY: Named for Jonas Nicolas Ahl, author of "De Muraena et Ophichtho", with the noun suffix *-ia* (neuter).

DISTRIBUTION: A single Caribbean species.

REMARKS: The controversy regarding generic synonymy of *Ahlia* has never involved a detailed osteological study. Those considering it synonymous with *Myrophis* (Parr, 1930: 8; Hildebrand, in Longley and Hildebrand, 1941: 17; Schultz and Woods, 1949: 171) did not consider the absence of vomerine teeth to represent a generic character, but it was assumed by Jordan and Davis (1891: 639), Myers and Storey (1939: 158), and Wade (1946: 199) that this warranted separation. Nelson (1966a: 398) considered *Ahlia* to be distinct on the basis of gill arch characters. The generic differences that I have identified are clearly related to feeding specialization in *A. egmontis*, viz., tooth loss, maxillary-pterygoid bracing, and gill arch reduction, yet the universality of these characters among the species of *Myrophis* suggests that the species of *Myrophis* form a natural group from which *Ahlia* is a specialized offshoot.

Cohen and Dean (1970) have recorded an interesting observation of offshore movements and a change in eye size accompanying the onset of sexual maturity in this species. Their observations were made off Honduras, approximately 145 km from shore. I have made similar observa-

tions within 1 km from land in the San Blas Archipelago, off the Atlantic coast of Panama.

*Muraenichthys* Bleeker

*Muraenichthys* Bleeker 1853b: 505. (Type species; *M. gymnopterus* Bleeker 1853, by original designation.)

*Scolecenchelys* Ogilby 1897: 246. Spelt *Scolenchelys* by other authors. (Type species; *Muraenichthys australis* Macleay 1881, by original designation.)

*Myroptera* Ogilby 1897: 247. (Type species; *Myroptera laticaudata* Ogilby 1897, by original designation.)

?*Aotea* Phillipps 1926: 533. (Type species; *Aotea acus* Phillipps 1926, by monotypy.)

DESCRIPTION: Body short to moderately elongate, tail generally longer than body, laterally compressed posteriorly; snout sub-conical to blunt, not deeply grooved on underside; posterior nostril either along edge of lip beneath a flap or opening into mouth; DFO from mid-trunk to well behind anus; pectoral fin absent; pop<sup>3</sup> present; LL ossicles continuous, well developed for a myrophin; dentition variable, teeth often multi-serial, either conical or blunt, dentition of vomer continuous with that of intermaxillary; skull sub-truncate posteriorly; SOC present; maxilla elongate, slender posteriorly (fig. 16); suspensorium nearly vertical; opercular series weakly ossified, subopercle generally rudimentary, produced posteriorly in some species (as in *Myrophis*, fig. 36); otic bulla weakly developed; PG short, not bracing maxillae, reduced and slender in one subgenus; HH separated from CH by a narrow gap; gill arches reduced, basibranchials absent, I<sub>2</sub> ossified and UP<sub>3</sub>-UP<sub>4</sub> fusion variable; pectoral girdle reduced to a slender CI and SCI; epipleural ribs on all precaudal vertebrae; CTP moderately developed.

ETYMOLOGY: From the Greek *μύρανα* an eel, and *ἰχθύς* (ichthys; masculine), fish.

DISTRIBUTION: Nineteen recognized species from the tropical, subtropical, and warm temperate Indo-Pacific Ocean, including a single species from the eastern south Pacific. Material exists of undescribed Red Sea and western Pacific species.

REMARKS: Subgeneric lines within *Muraenichthys* were indicated by McCosker (1970) but were not designated pending a thorough osteological study. My examination and comparison of M.

*gymnopterus*, *M. chilensis*, and *M. macropterus* did not uncover osteological differences comparable to those used to separate other closely related ophichthid genera. This result was unexpected in that the external morphology differs considerably within the genus, including differences in snout form (from blunt to acute), in body depth (15-50 times in total length), in the number and position of head pores, in dentition, and in the character of the posterior nostril. Sub-generic lines may be identified in the following manner:

Posterior nostril opens on the outer lip as an elongate slit with an anterior flap; a single pore between the anterior and posterior nostrils; jaw teeth usually in bands, intermaxillary teeth in a patch; UP<sub>3</sub>-UP<sub>4</sub> fused in species examined; snout usually blunt; body usually stout, its depth ca. 15-25 in TL .....  
 ..... Subgenus *Muraenichthys* Bleeker

Posterior nostril opens into mouth, covered by an exterior valvular flap; two pores between nostrils; jaw teeth uniserial or biserial, intermaxillary teeth not in a broad patch; UP<sub>3</sub>-UP<sub>4</sub> separate in species examined; snout usually acute; body moderately elongate, its depth usually more than 25 in TL .....  
 ..... Subgenus *Scolecenchelys* Ogilby

The subgenus *Muraenichthys* includes *M. gymnopterus* Bleeker (the type species), *M. hattae* Jordan and Snyder, *M. schultzei* Bleeker, and possibly *M. macrostomus* Bleeker, *M. philippinensis* Schultz and Woods, *M. sibogae* Weber and de Beaufort, and *M. thompsoni* Jordan and Richardson. The subgenus *Scolecenchelys* includes *M. australis* Macleay\* (the type species), *M. chilensis* McCosker, *M. acutirostris* Weber and de Beaufort, *M. cookei* Fowler, *M. gymnotus* Bleeker, *M. macropterus* Bleeker, *M. breviceps* Günther, and possibly *M. iredalei* Whitley. Also included in *Muraenichthys*, but not here allocated to a subgenus, are *Myropterura laticaudata* Ogilby, *Chilorhinus vermiformis* Peters, *Muraenichthys devisi* Fowler, *M. xorae* Smith\*, and *M. godeffroyi* Regan. My specimens of *M. macropterus* disagreed with Nelson's (1966a) description in having an unfused UP<sub>3</sub>-UP<sub>4</sub>.

The genera *Muraenichthys*, *Schultzidia*, and *Schismorhynchus* display obvious similarities attributable to a common ancestry. Primitive and advanced conditions of certain characters may be identified among the approximately 24 species

involved (many of the species included are known to me only from the literature and not from specimens). For example, postulated primitive conditions include the moderately elongate body, sub-conical snout, posterior nostril opening into the mouth, numerous head pores, uniserial or biserial conical teeth, presence of the SO crest, posterior development of the subopercle, separate hypohyals, ossified second infrapharyngobranchial, separate UP<sub>3</sub>-UP<sub>4</sub>, and conspicuous cleithrum and supracleithrum. Species of the subgenus *Scolecenchelys* are clearly the most primitive, with the species of the subgenus *Muraenichthys*, and *Schultzidia* and *Schismorhynchus* as specialized offshoots. The development of transverse processes on the caudal vertebrae, shared by these genera, is unique among the Myrophinae and without apparent antecedents in more primitive genera such as *Myrophis*.

*Aotea*, type species *A. acus*, was described by Phillipps (1926) on the basis of a partially digested specimen from New Zealand waters, and placed in *Muraenichthys* by Castle (1967). Whitley (1968) placed *A. acus* in the synonymy of *Muraenichthys breviceps* Günther, yet Phillipps (1926: 533-534) characterized *A. acus* as having "fins absent" and "a hard folded portion beneath body posterior to head apparently indicating gill-openings . . .", both of which would exclude *Aotea* from the subfamily Myrophinae. Phillipps' sketchy description of *A. acus* does not obviously agree with any known ophichthine genus, but best fits *Apterichtus*, *Ichthyapus*, and *Cirricaecula*. Further examination may discover that *Aotea acus* is a species of *Apterichtus* in that the species of the latter two genera are not known from even as far south as Australian waters.

#### *Myrophis* Lütken

- Myrophis* Lütken 1851: 14. (Type species; *M. punctatus* Lütken 1851, by monotypy.)  
*Paramyrus* Günther 1870: 51. (Type species; *Conger cylindroideus* Ranzani 1838, by Jordan and Davis (1891) as first revisers.)  
*Holopterura* Cope 1871: 482. (Type species; *H. plumbea* Cope, 1871, by monotypy.)  
*Hesperomyrus* Myers and Storey 1939: 157. (Type species: *H. fryi* Myers and Storey 1939 = *Myrophis vafer* Jordan and Gilbert, by original designation.)

DESCRIPTION: Body stout to moderately elongate, laterally compressed throughout; snout sub-

conical to conical and moderately elongate; eye moderate; posterior nostril along edge of lip beneath a flap or opening into mouth; DFO before mid-trunk region; pectoral fin moderately developed, longer than eye;  $pop^3$  present; teeth conical, uniserial or biserial in jaws and vomer; skull subtruncate posteriorly (fig. 5); SOC present; maxilla elongate, slender posteriorly (fig. 30B); subopercle produced posteriorly as a posteroventral border to the opercle (fig. 36); otic bulla weakly developed; PG short, not bracing maxilla;  $H_3$  cartilaginous,  $UP_3$ - $UP_4$  fused in one species; Cl and SCl slender, Sc, Co, and an actinost (?) well developed; epipleural ribs limited to anterior-most 15-20 vertebrae; CTP absent.

ETYMOLOGY: From the Greek  $\muύρος$ , *Myrus*, and  $ὄφις$  (ophis; masculine), snake.

DISTRIBUTION: A circumtropical genus of nine nominal species. Included are: *Myrophis punctatus* Lütken (WA), *M. australis* Castelnau (IP)\*, *M. cheni* Weng (IP)\*, *M. lepturus* Kotthaus (IP)\*, *M. platyrhynchus* Breder (WA)\*, *M. vafer* Jordan and Gilbert (EP), *Conger uropterus* Temminck and Schlegel (IP), *C. cylindroideus* Ranzani (EA)\*, *Holopterura plumbea* Cope (EA). *Incertae sedis*: *Myrophis frio* Jordan and Davis (WA)\*.

REMARKS: Schultz, et al. (1953: 68) erroneously included *Parabathymyrus* Kamohara in the synonymy of *Myrophis*. D. Smith (1971) recognized it as a valid congrid genus of the subfamily Bathymyrinae.

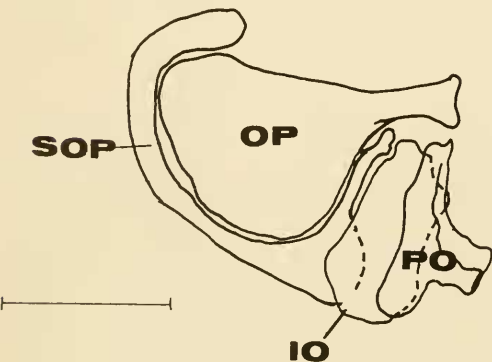


Figure 36. Opercular series of *Myrophis vafer*, SIO 68-242. Right side, distal view. Scale represents 1 mm. Abbreviations are: IO, interopercle; OP, opercle; PO, preopercle; SOP, subopercle.

Castle (1963: 16) has discussed the identity of the congrid *Gnathophis heterognathus* (Bleeker) which has been erroneously included in *Myrophis* by recent authors.

#### *Neenchelys* Bamber

*Neenchelys* Bamber 1915: 479. (Type species; *N. microtretus* Bamber 1915, by monotypy.)

DESCRIPTION: Body moderately elongate, compressed posteriorly; body shorter than tail; snout sub-conical; eye moderate; posterior nostril an elongate slit before lower margin of orbit; DFO before mid-trunk; pectoral fin moderately developed, longer than eye;  $pop^3$  absent; teeth conical, uniserial except at vomerines and intermaxillary; skull rounded posteriorly; nasal condition unknown; SOC absent; maxilla elongate and slender posteriorly; subopercle not developed posteriorly (fide Nelson 1966b, fig. 1e); otic bulla weakly developed;  $B_1$  rudimentary,  $I_2$  ossified,  $UP_3$ - $UP_4$  separate; pectoral girdle developed, SCl, Cl, Sc, Co, and an actinost (?) present; epipleural rib condition unknown.

ETYMOLOGY: Presumably from the Greek  $νευ$ , new, and  $ἐνχελύς$  (enchelys; feminine or masculine, treated as masculine by Bamber), eel.

DISTRIBUTION: Two species, *N. microtretus* Bamber\* from the Red Sea, and *N. buitendijki* Weber and de Beaufort\* from the Indian Ocean.

REMARKS: Specimens of *Neenchelys* were unavailable for this study. The description is prepared from Nelson's (1966b) osteological and Mohamed's (1958) morphological description of *N. buitendijki*. Nelson (1967) noted the presence of overlapping branchiostegals in the holotype of *N. microtretus* (apparently the only known specimen) but did not compare it with *N. buitendijki*.

Nelson (1966b: 323), in commenting on Wade's (1946) description of *Pseudomyrophis micropinna*, stated that "there is no character significant enough to maintain *Pseudomyrophis* as a genus distinct from *Neenchelys*. *P. nimius*, on the other hand, seems distinctive enough to be placed in a genus of its own." My osteological examination of the species of *Pseudomyrophis*, which I have found to be congeneric, allows further comment on this relationship. The two genera show certain similarities in morphology and habitat (living in mud bottoms in moderately deep water) and are more closely related to each other than to other genera. Osteological similarities include the shapes of the neurocrania,

pterygoids, maxillae, gill arches, hyoid arches, and caudal vertebrae. The characters used in the generic key to separate these genera may be expanded in the following manner:

DFO in anterior trunk region; snout conical; pectoral fin well developed,  $\cong$  snout; pop<sup>3</sup> absent; subopercle small, sub-rectangular; (pop<sup>3</sup> and subopercle condition of *N. microtretus* unknown) .....*Neechelys*

DFO in posterior trunk region; snout broad, tumid; pectoral fin minute,  $\leq$  eye; pop<sup>3</sup> present; subopercle produced posteriorly along ventral and posterior margins of opercle .....*Pseudomyrophis*

*Pseudomyrophis* Wade

*Pseudomyrophis* Wade 1946: 199. (Type species; *P. micropinna* Wade 1946, by original designation.)

DESCRIPTION: Body moderately to extremely elongate, laterally compressed throughout; snout broad, tumid; eye small to moderate; posterior nostril an elongate slit before lower margin of orbit; DFO behind mid-trunk; pectoral fin minute, smaller than eye; pop<sup>3</sup> present; teeth conical, uniserial throughout, except at anterior vomer and intermaxillary; skull rounded posteriorly; nasals ossified along canal only, nasal cartilage weakly developed; SOC absent; maxilla elongate, slender posteriorly; subopercle similar to *Myrophis* (Fig. 36), produced posteriorly as a slender posteroventral border to opercle; otic bulla weakly developed; PG short, not produced anteriorly; B<sub>1</sub> and I<sub>2</sub> ossified, UP<sub>3</sub>-UP<sub>4</sub> separate; pectoral girdle reduced to Cl and SCl (and fractional Co? in *P. micropinna*); epipleural ribs on all precaudal vertebrae.

ETYMOLOGY: From the Greek ψευδής (pseudēs), false, -o-, and *Myrophis* (masculine), a genus of ophichthids.

DISTRIBUTION: Two New World species, *P. nimius* Böhlke (Caribbean) and *P. micropinna* Wade (eastern Pacific).

REMARKS: The species of *Pseudomyrophis* are strikingly different in body depth and head length, yet an osteological comparison did not uncover differences that are clearly generic. Other proportional differences are also related to the extreme elongation of *P. nimius*. The mean difference in vertebral number between species (ca. 50) is less than that between species

of *Phaenomonas* (ca. 70). Both species are apparently adapted to soft mud bottoms in water relatively deep for ophichthids (*P. micropinna* from depths of 45-60 fms, *P. nimius* to 400 fms).

*Schismorhynchus* McCosker

*Schismorhynchus* McCosker 1970: 509. (Type species; *Muraenichthys labialis* Seale 1917, by original designation.)

DESCRIPTION: General characteristics those of *Muraenichthys*. Differences include: body moderately elongate; body shorter than tail; snout conical, elongate, with a prominent toothed groove on underside; anterior nostril an elongated tube as long as eye; posterior nostril opens into mouth; DFO in posterior trunk region; pop<sup>3</sup> and median interorbital pore absent; teeth conical, uniserial; maxilla broad, not becoming slender posteriorly; subopercle produced posteriorly as in *Myrophis* (fig. 36); suspensorium anteriorly inclined; HH fused to CH (or absent?), GH rudimentary; gill arches extremely reduced, B<sub>1</sub>, H<sub>3</sub>, and I<sub>2</sub> absent, UP<sub>3</sub>-UP<sub>4</sub> fused, lower tooth plate elongate (see Nelson, 1966a: figs. 14-15); pectoral girdle reduced to a slender Cl.

ETYMOLOGY: From the Greek σχισμή (schisme), cleft, and ριζός (latinized as rhynchus, masculine in accordance with item 30(a)(3) of the International Code of Zoological Nomenclature), nose.

DISTRIBUTION: A single species, widespread in the central and western Pacific ocean.

*Schultzidia* Gosline

*Schultzidia* Gosline 1951a: 309. Described as a subgenus of *Muraenichthys* Bleeker. (Type species; *Muraenichthys johnstonensis* Schultz and Woods 1949, by original designation.)

DESCRIPTION: General characteristics those of *Muraenichthys*. Differences include: body stout to moderately elongate, body shorter than tail; posterior nostril opens into mouth; DFO behind anus; pop<sup>3</sup> absent; teeth absent on vomer, absent or imbedded on intermaxillary, those on maxilla and dentary minute or villiform; SOC absent, SO extends anteriorly to frontals, completely separating parietals; opercular series rudimentary, subopercle not produced posteriorly; PG slender; hyoid rudimentary, HH separated from CH by a gap, UH fragmentary, separated medially; gill arches extremely reduced, B<sub>1</sub> and I<sub>2</sub>

absent, UP<sub>3</sub>-UP<sub>4</sub> fused, tooth plates elongate and vermiculated; CTP weakly developed.

ETYMOLOGY: Named for Leonard P. Schultz, ichthyologist, with the assumed noun suffix *-idia* (feminine).

DISTRIBUTION: Two central and western Pacific species, described as *Muraenichthys johnstonensis* Schultz and Woods, and *M. retropinnis* Seale.

#### Subfamily Ophichthinae

DIAGNOSIS: Gill opening variable, mid-lateral to entirely ventral and longitudinal, generally elongate and unstricted; DFO variable, from nape to behind anus; tail tip generally a hard finless point, rudimentary rays visible in certain genera; nasals ossified, generally well developed, but reduced or absent in certain genera; CH divided into a short median and longer distal portion, the median section connecting to the CH by a cartilaginous splint (see fig. 17A); UH generally continues posteriorly from basal plate as a slender ossified spike; all branchiostegal rays originate either in association with hyoid or before level of EH tips; gill arch skeleton variably developed, first basibranchial always ossified, second through fourth generally present in either a cartilaginous or rudimentary condition, C<sub>5</sub> present in several genera; coloration variable, banded, barred, striped, spotted, or uniform patterns.

#### Tribe Callechelyini

TYPE GENUS: *Callechelys* Kaup, 1856

DIAGNOSIS: Body (head and trunk) and tail moderately elongate, laterally compressed; body longer than tail; snout acute, rounded at tip; lower jaw included; eye small; posterior nostril opens into mouth; GO low lateral to entirely ventral, converging forward, length much greater than isthmus width; dorsal fin originating on nape; pectoral fin absent; tail tip a hard finless point; head pores reduced, pop<sup>3</sup> and tp<sup>2</sup> absent; LL ossicles nearly continuous; teeth conical, jaw teeth uniserial, those of vomer separated from those of intermaxillary by a gap; skull short, sloping posteriorly, its height ca. 3 or less in its length (fig. 7); orbit moderately developed; SO rounded, without a posterior projection; PG slender, elongate, free and tapering posteriorly; margin of opercular series irregularly ossified, with cartilaginous gaps; suspensorium nearly vertical; otic bulla well developed; hyoid stout; branchiostegal rays numerous; gill arches re-

duced, C<sub>5</sub> absent, UP<sub>3</sub>-UP<sub>4</sub> separate; pectoral girdle reduced to CI, SCI, and 1 or 2 rod-shaped elements; IM bones, ribs, and CTP developed; precaudal vertebrae more numerous than caudal; coloration variable, either striped, barred, spotted, mottled, or uniform.

REMARKS: The Callechelyini constitute the most distinct and compact of ophichthid tribes. Available material or radiographs of 19 of the 21 species of Callechelyini has allowed an in depth study of this tribe. The results of two computer-programmed numerical taxonomic evaluations of this tribe are presented in the discussion section. Several important morphological and osteological characters of the species are listed in Table 8.

#### *Aprognathodon* Böhlke

*Aprognathodon* Böhlke 1966: 99. (Type species; *A. platyventris* Böhlke 1966, by original designation.)

DESCRIPTION: Anterior nostril tubular; snout moderate, rounded at tip; median groove absent on underside of snout; intermaxillary teeth absent, vomerine teeth present; DFO above SO; anal fin present; 3 supraorbital pores; neurocranium well rounded, highest anterior to frontal-parietal suture; hyoid arch very stout, inflexible along CH-EH suture; HH absent; branchiostegal rays numerous, along arch, often joined basally, distal 4-6 rays along EH broadened basally; UH a simple cartilaginous projection posteriorly, basal plate ossified; gill arches stout, H<sub>3</sub> partially or completely ossified; pectoral girdle contains CI, SCI, and 2 rod-shaped elements; body coloration strongly banded longitudinally.

ETYMOLOGY: From the Greek  $\alpha$ , without,  $\pi\rho\acute{o}$  (pro), forward,  $\gamma\nu\acute{\alpha}\theta\omicron\varsigma$  (gnathos), jaw, and  $\acute{o}\delta\acute{o}\nu$  (odon; masculine), tooth, in reference to the lack of intermaxillary dentition.

DISTRIBUTION: A single western Atlantic species, known from the Bahamas through the Lesser Antilles to Venezuela.

#### *Callechelys* Kaup

*Callechelys* Kaup 1856: 51 (28). (Type species; *C. guichenoti* Kaup 1856 = *Dalophis marmorata* Bleeker 1853, by monotypy.)

*Cryptopterygium* Ginsburg 1951: 482. (Type species; *Cryptopterygium holochroma* Ginsburg 1951, by original designation.)

DESCRIPTION: Anterior nostril tubular; snout short, rounded at tip; a median groove on underside of snout (Fig. 32A); intermaxillary and vomerine teeth present; DFO above SO; anal fin present; 3 supraorbital pores; neurocranium well rounded, highest anterior to level of frontal-parietal suture (fig. 7); hyoid arch stout, moderately flexible along CH-EH suture; HH separated from CH by a narrow gap; branchiostegal rays numerous, along arch; distal rays along EH broadened basally in some species; UH either a simple slender filament posteriorly, or split into two divergent rays; H<sub>3</sub> cartilaginous; pectoral girdle contains CI, SCl, and either one or two rod-shaped elements; coloration variable, either uniform, spotted, mottled, or banded.

ETYMOLOGY: Kaup (1856a, b) did not give the derivation of the generic name nor did he designate its gender. From his description (1856b: 28), "this handsome eel . . .", one must assume that he intended the generic name to be derived from *καλὸς* (beauty) and *ἔχελυς* (enchelys, eel) which is feminine, but according to Liddell and Scott (1801), was later also masculine. Bleeker (1865), as first reviser, further confused matters by recognizing *Dalophis marmorata* Bleeker as *Callechelys marmoratus* and also describing *Callechelys melanotaenia*. To date, the gender of *Callechelys* has not been established, although the most recent revisers (McCosker and Rosenblatt, 1972) have regarded *Callechelys* as masculine.

DISTRIBUTION: A cosmopolitan genus with 15 tropical and subtropical species. Nominal species include: *Callechelys bilinearis* Kanazawa (WA), *C. cliffi* Böhlke and Briggs (EP), *C. eristigmus* McCosker and Rosenblatt (EP), *C. galapagensis* McCosker and Rosenblatt (EP), *C. luteus* Snyder (IP), *C. melanotaenia* Bleeker (IP), *C. muraena* Jordan and Evermann (WA), *C. nebulosus* Smith (IP), *C. perryae* Storey (WA, EA), *C. striatus* Smith (IP), *Ophichthys bitaeniatus* Peters (IP)\*, *Cryptopterygium holochroma* Ginsburg (WA), *Caecula leucoptera* Cadenat (EA)\*, *Dalophis marmorata* Bleeker (IP), *Gordiichthys springeri* Ginsburg (WA).

REMARKS: Numerous authors (Günther, 1910: 404; Pellegrin, 1912; Storey, 1939: 63; Smith, 1957: 83; McCosker and Rosenblatt, 1972: 22) have discussed the validity of *C. guichenoti*, the generic type, with the majority supporting its synonymy with *C. marmoratus*. Marie-Louise

Bauchot of the Paris Museum has kindly furnished measurements and a radiograph of the type specimen (MNHN 2126) of *C. guichenoti*. Its morphometry and osteology (183 vertebrae and a single pectoral girdle horizontal element) are further evidence of its synonymy with *C. marmoratus*.

Subgeneric lines within *Callechelys* were suggested by McCosker and Rosenblatt (1972). They recognized two major groups, one containing species with a simple urohyal and a single rod-shaped pectoral element (fig. 19L) and another with species having the urohyal split posteriorly into two slender divergent rays and two rod-shaped pectoral elements (as in *Aprognathodon*, fig. 19M). A third can be recognized, which possesses a mosaic of characters, including slightly broadened branchiostegal rays along the epiphyal, and urohyal and pectoral girdle conditions that do not conform to either of the above groups. Programs REGROUP and WVGM showed little affinity between *C. nebulosus* of this last group and the remainder of the genus. It appears that the simple urohyal, broadened rays, and paired girdle elements are primitive conditions within the Callechelyini, characters shared by *C. nebulosus* and *C. springeri*.

#### *Letharchus* Goode and Bean

*Letharchus* Goode and Bean 1882: 437. (Type species *L. velifer* Goode and Bean 1882, by original designation.)

DESCRIPTION: Anterior nostril a hole, its rim not raised; snout moderate, acute, not rounded at tip; median groove on underside of snout absent (fig. 32b); intermaxillary and vomerine teeth present; DFO above epiotics; anal fin absent; four supraorbital pores; neurocranium depressed, not rounded across parietal-frontal region, highest at frontal-parietal suture; hyoid arch stout, flexible along CH-EH suture, HH separated from CH by a gap; branchiostegal rays numerous, slender, all along arch; UH a slender filament posteriorly; H<sub>3</sub> cartilaginous; pectoral girdle contains CI, SCl, and 2 rod-shaped elements; body coloration uniformly dark, contrasting strongly with the white dorsal fin.

ETYMOLOGY: From the Greek *λησθαι* to forget, and *ἄρχος* (archos; masculine), anus, in reference to the lack of an anal fin.

DISTRIBUTION: Known from three New World species: *L. velifer* from the western Atlantic

(North Carolina to the northern Gulf of Mexico), *L. aliculatus* McCosker from off Brazil, and *L. rosenblatti* McCosker from the eastern Pacific.

REMARKS: The genera *Letharchus* and *Paralettharchus* were recently revised by McCosker (1974). The species of *Letharchus* form a unique and distinctive offshoot from the generalized callechelyin condition in their combination of anal fin absence, non-tubular nostrils, an additional supra-orbital pore, and the acute snout, differing markedly from the characters of other genera within the tribe. *Letharchus pacificus* Osburn and Nichols and *L. opercularis* Myers and Wade are obviously similar to the above species in lacking an anal fin, and probably for that reason were assumed by their describers to be congeneric with *L. velifer*. After examining considerable material and the types of these five species I have concluded that *L. opercularis* and *L. pacificus* represent a separate generic line within the Callechelyini.

The osteological description of *Letharchus* is based on the eastern Pacific species in that material of *L. velifer* was unavailable for dissection.

#### *Leuropharus* Rosenblatt and McCosker

*Leuropharus* Rosenblatt and McCosker 1970: 502. (Type species; *L. lasiops* Rosenblatt and McCosker 1970, by original designation.)

DESCRIPTION: Anterior nostril tubular; snout short, rounded at tip; median groove on underside of snout absent; snout, nape, and much of surface of jaws papillate; intermaxillary teeth present, vomerine teeth absent; DFO above SO; anal fin present; three supraorbital pores; neurocranium well rounded, highest anterior to frontal-parietal suture; HH separated from CH by a gap; branchiostegal rays numerous, slender, and along arch; H<sub>3</sub> cartilaginous; pectoral girdle contains Cl, SCl, and 2 rod-shaped elements; body coloration nearly uniform, median fins white.

ETYMOLOGY: From the Greek *λευρός* (leuros), smooth, and *φάρος* (pharos; neuter), plow, in reference to the toothless vomer.

DISTRIBUTION: A single species, known only from the type specimen from Manzanillo Bay, western Mexico.

#### *Paralettharchus* McCosker

*Paralettharchus* McCosker 1974: 620. (Type species; *Letharchus pacificus* Osburn and Nichols,

1916, by original designation.)

DESCRIPTION: Anterior nostril tubular; snout short, rounded at tip; median groove on underside of snout absent; LL ossicles block-like cylinders, not heavily fractionated (compare figs. 22H and 22I); intermaxillary and vomerine teeth present; GO with a deep anterolateral pocket; DFO above SO; dorsal fin elevated; anal fin absent; three supraorbital pores; neurocranium well rounded, highest anterior to frontal-parietal suture; hyoid arch stout, only slightly flexible along EH-CH suture; HH separated from CH by a narrow gap; branchiostegal rays numerous, along arch, distal rays along epihyal broadened basally; UH a simple slender filament posteriorly; H<sub>3</sub> cartilaginous; pectoral girdle contains Cl, SCl, and 2 rod-shaped elements; coloration nearly uniform to mottled.

ETYMOLOGY: From the Greek *πάρᾱ* (para), near, and *Letharchus* (masculine), a related genus.

DISTRIBUTION: Known from two eastern Pacific species, *P. opercularis* (Myers and Wade), a Galapagos endemic, and *P. pacificus* (Osburn and Nichols), ranging from Baja California to Costa Rica.

REMARKS: As mentioned in the remarks on *Letharchus*, the above-mentioned species are not congeneric with *L. velifer*. Schultz and Barton (1960) placed *L. opercularis* in the synonymy of *L. pacificus*, however McCosker (1974) provisionally recognized the Galapagos population as distinct on the basis of the difference in the mean vertebral number (95% confidence limits: *P. opercularis* 172.7 - 176.6, *P. pacificus* 158.5 - 162.3).

#### Tribe Sphagebranchini

TYPE GENUS: *Caecula* Vahl 1794, the senior objective synonym of *Sphagebranchus* Bloch, 1795 (see following remarks).

DIAGNOSIS: Body (head and trunk) and tail moderately elongate, cylindrical, often compressed posteriorly; body either nearly equal to or shorter than tail; snout pointed, often broad and depressed; lower jaw included; posterior nostril opens into mouth in most genera; GO entirely ventral; median fins either very low or absent; pectoral fin absent; tail tip sharply pointed; head pores well developed, tp<sup>2</sup> and pop<sup>3</sup> generally, and pop<sup>4</sup> sometimes present; LL ossicles



continuous; teeth conical, not caniniform, and generally uniserial; intermaxillary teeth separated by a gap from those of vomer; neurocranium elongate, generally depressed and truncate posteriorly; orbit reduced; otic bulla moderately to well developed; hyoid arch generally slender; branchiostegal rays few to numerous, generally closely associated with hyoid; gill arches reduced, C<sub>5</sub> absent in most genera; intramuscular bones, ribs, and caudal transverse processes well developed; precaudal either nearly equal to or more numerous than caudal vertebrae; coloration generally uniform, or darker dorsally.

REMARKS: Included among the genera of the Sphagebranchini are the most frustrating and problematical of ophichthid taxa. Their nearly complete lack of superficial characters has resulted in a history of repeated lumping and splitting. Further confusion stems from the inadequate and misleading descriptions of the two oldest generic names, *Caecula* Vahl (1794) and *Sphagebranchus* Bloch (1795). Gosline (1951: 311) summarized the problem in stating that "the definition, and consequently the limits, of the genus *Caecula* are agreed upon by no two authors as far as I know."

The tribal name Sphagebranchini is derived from Swainson's (1838) family name Sphagebranchidae. Swainson's family name was subsequently rejected (see page 10) long before *Sphagebranchus* Bloch (1795) was shown to be a junior objective synonym of *Caecula* Vahl (1794) (see Böhlke and McCosker, 1975). The family-group name Caeculidae has not appeared in the ichthyological literature. In accordance with Article 40 of the International Code of Zoological Nomenclature (1964), the family-group name Sphagebranchini therefore has priority as the tribal name, with *Caecula* as the type genus of the tribe.

*Achirophichthys* Bleeker

*Achirophichthys* Bleeker 1865: 41. (Type species; *A. typus* Bleeker 1865, by original designation.)

DESCRIPTION (based on Bleeker, 1865, and Weber and de Beaufort, 1916): Body stout, slightly longer than tail; snout pointed; eye small; anterior nostril not tubular, posterior nostril opens into mouth; lips with one row of minute tubercular papillae; DFO slightly behind GO; GO low lateral to inferior; teeth conical, long and nearly caniniform anteriorly and along vomer, uniserial on vomer, biserial on maxilla.

ETYMOLOGY: From the Greek  $\alpha\chi\iota\rho\phi\iota\chi\theta\iota\varsigma$  (achir), without hands, and *Ophichthys*, (masculine), the amended spelling of *Ophichthus*.

DISTRIBUTION: A single western Pacific species.

REMARKS: An osteological diagnosis of *Achirophichthys* is not included in this study in that material of *A. typus*, the generic type, was unavailable. *A. kampeni* (Weber and de Beaufort), its sole described congener, is herein referred to *Lamnostoma*. Jordan and Davis (1891: 636) suggested that *A. typus* might be the young of *Brachysomophis crocodilinus*, but subsequent authors have neither accepted nor commented upon this action. Weber and de Beaufort (1916) considered *Achirophichthys* to be a subgenus of *Brachysomophis*. This too was ignored by most subsequent authors. Their description of *A. typus*, based on the type specimen, strongly indicates that it is congeneric with *A. kampeni*, which if true, would place *Achirophichthys* in the synonymy of *Lamnostoma*.

*Apterichtus* Duméril

*Caecilia* Lacépède 1800: 134. Preoccupied by *Caecilia* Linnaeus, a genus of Amphibia. (Type species; *C. branderiana* Lacépède 1800, by monotypy.)

*Apterichtus* Duméril 1806: 331. Also spelled *Apterichthys*, *Apterichthus*, *Apterichthe*, and *Apterichtes* by other authors. (Type species; *Muraena caeca* Linnaeus 1758, by monotypy.) *Typhlotes* Fischer 1813: 81. A replacement name for *Caecilia* Lacépède, preoccupied.

*Branderius* Rafinesque 1815: 93. A replacement name for *Caecilia* Lacépède, preoccupied.

*Ophisurapus* Kaup 1856a: 52. (Type species; *O. gracilis* Kaup 1856, by monotypy.)

*Ophisuraphis* Kaup 1856b: 29. *Emend. pro Ophisurapus* Kaup 1856a.

Verma Jordan and Evermann 1896: 374. (Type species; *Sphagebranchus kendalli* Gilbert 1889, by original designation.)

?*Microrhynchus* Blache and Bauchot 1972: 728. Preoccupied by *Microrhynchus* Dejean 1821, a genus of lepidoptera, as well as mammalia (Jordan 1834), crustacea (Bell 1835), aves (Lesson 1843) and vermes (Kepner 1935). (Type species; *Sphagebranchus foresti* Cadenat and Roux 1964, by original designation.)

DESCRIPTION: Body very elongate, cylindrical, and pointed at both ends; body and tail nearly subequal; snout pointed, sub-conical, grooved

and flattened on underside; lips without barbels; eye moderately developed; anterior nostril tubular, posterior nostril a horizontally ovate slit outside of mouth; GO ventral, converging forward; isthmus short; all fins absent;  $tp^2$  and  $pop^4$  presence variable among species; teeth pointed, uniserial in jaws, and largest at intermaxillary which is separated from those of vomer by a short gap; skull slightly depressed, sub-truncate to rounded posteriorly; orbit reduced; nasals and nasal cartilage developed; SOC short and blunt posteriorly; maxilla pointed posteriorly; opercular margins entire; suspensorium anteriorly inclined, jaw angle ca.  $100^\circ$ ; PG slender, pointed and very reduced; hyoid arch slender, HH separated from CH by a gap; branchiostegal rays closely associated with hyoid; UH cartilaginous posteriorly;  $C_5$  absent,  $UP_3$ - $UP_4$  separate; CI broad, SCI reduced, Co and Sc absent; posterior trunk parapophyses with an anterior marginal projection (fig. 33).

ETYMOLOGY: From the Greek  $\alpha\pi\tau\epsilon\phi\acute{o}\nu$  (apteron), without fins, and (ichthys, more correctly written ichthys; masculine), fish.

DISTRIBUTION: From 10-12 described and valid species, represented in all tropical oceans. Böhlke (1968) provisionally reviewed the species of *Verma* (= *Apterichtus*). The genus *Apterichtus* can be expanded to include: *Muraena caeca* Linnaeus (M), *Caecula gymnocelus* Böhlke (EP), *C. monodi* Roux (EA)\*, *C. equatorialis* Myers and Wade (EP), *Sphagebranchus klanzingai* Weber (IP), *S. flavicaudus* Snyder (IP), *S. kendalli* Gilbert (WA), *Verma ansp* Böhlke (WA), *Ophisurapus gracilis* Kaup (EA)\*, *Ophichthys anguiformis* Peters (EA)\*, and possibly *Sphagebranchus lor-esti* Cadenat and Roux (EA)\* and *Microrhynchus epinepheli* Blache and Bauchot (EA)\*.

REMARKS: Blache and Bauchot (1972) recognized *Verma* as distinct from *Apterichtus* on the basis of a minor difference in posterior nostril location. Through the kindness of Enrico Tortonese I have examined a specimen of the Mediterranean *Apterichtus caecus*, and have concluded that it is clearly congeneric with the Atlantic and Pacific species previously referred to *Verma*. *Microrhynchus* Blache and Bauchot (1972) is based upon two species known only from the holotypes. Both were unavailable for study. Their sketchy description of the external morphology of the species, upon which the present study is based, does not provide characters which would allow their generic separation from

*Apterichtus*, or possibly *Ichthyapus*. Should *Microrhynchus* prove to be a valid genus a substitute name will be required.

#### Caecula Vahl

*Caecula* Vahl 1794: 149. (Type species; *C. pterygera* Vahl 1794, by original designation.)

*Sphagebranchus* Bloch 1795: 88. (Type species; *S. rostratus* Bloch 1795 = *Caecula pterygera* Vahl 1794, by monotypy.)

DESCRIPTION: Body moderately elongate, cylindrical, compressed posteriorly; body and tail nearly subequal; snout pointed, depressed, and broad dorsally, grooved and flattened on underside; eye moderate; anterior nostril flush with snout anteriorly, produced as a tube posteriorly, posterior nostril associated with a barbel; GO entirely ventral, converging anteriorly, much longer than isthmus, and with an anterolateral duplication forming a deep pouch; DFO slightly behind GO;  $pop^3$  and  $tp^2$  present,  $pop^4$  absent; teeth conical and uniserial, largest at intermaxillary which is widely separated from those of vomer; skull depressed, broad, and truncate posteriorly; orbit extremely reduced; nasals and nasal cartilage well developed; SOC a short broad point posteriorly; maxilla elongate, pointed posteriorly; coranoid process of articular moderately enlarged; operculum well developed, preoperculum narrow and thin, their margins entire; suspensorium nearly vertical; hyomandibular broad, expanded posterodorsally and anteriorly, strongly ridged; otic bulla weakly developed; PG slender, pointed at each end, and braced against hyomandibular by a posteromedial extension; hyoid arch slender; HH separated from CH by a gap; branchiostegal rays numerous, flat and unbranched, loosely associated with hyoid; outermost rays along epihyal slightly broadened; UH a slender filament posteriorly;  $C_5$  absent,  $UP_3$ - $UP_4$  separated, anterior half of  $B_1$  ossified; CI, SCI, Sc and Co present.

ETYMOLOGY: A diminutive of the Latin caecus, blind, regarded as feminine.

DISTRIBUTION: Two western Pacific species.

REMARKS: Various species have been haphazardly assigned to *Caecula* to such an extent that it has become a catch-all for most finned and finless ophichthids lacking pectoral fins. Smith (1964) redescribed the type of *C. pterygera* and began the dissection of this confusing assemblage. Smith erred in presuming *C. pterygera* and

*Lamnostoma pictum* to be synonymous, and in fact, congeneric. Osteologically these genera are similar in their coronoid processes, hyoid, gill arch, and nostril conditions, but differ trenchantly in their neurocrania.

Blache and Bauchot (1972) placed the type species of *Sphagebranchus*, *S. rostratus* Bloch, in *Caecula*. Böhlke and McCosker (1975) considered the type species of those genera to be conspecific, and suggested that the collection locality of *S. rostratus* ("river in Surinam") was erroneous.

#### *Cirricaecula* Schultz

*Cirricaecula* Schultz 1953: 49. Type species; *C. johnsoni* Schultz 1953, by original designation.)

DESCRIPTION: General characters those of *Ichthyapus*. Differences include: body and tail nearly subequal; numerous cirri along edge of upper lip, a prominent barbel between the nostrils; anterior nostril nearly flush with snout anteriorly, slightly produced as a tube posteriorly; GO entirely ventral, consisting of 2 parallel longitudinal slits with thin medial membranes; isthmus minute;  $pop^4$  and  $tp^2$  present; otic bulla weakly developed; PG slender, pointed at each end; hyoid arch slender, HH separated from CH by a gap, UH a slender filament posteriorly;  $C_5$  ossified,  $UP_3$ - $UP_4$  fused; pectoral girdle reduced to a ventrally located CI pair which are broad and anteriorly expanded (fig. 19); CTP strongly developed.

ETYMOLOGY: From the Latin *cirrus*, tendril, and *Caecula* (feminine), a related genus.

DISTRIBUTION: A single central Pacific species, known only from the type series collected at Eniwetok, Marshall Islands.

#### *Hemerorhinus* Weber and de Beaufort, *incertae sedis*

*Hemerorhinus* Weber and de Beaufort 1916: 280. (Type species; *Sphagebranchus heyningi* Weber 1913, by original designation.)

DESCRIPTION: Body moderately elongate, cylindrical, pointed at each end; body longer than tail; snout pointed, grooved on underside; eye small; anterior nostril flush with snout; posterior nostril below eye, a long slit in upper lip; GO inferior, vertical; vertical fins low;  $tp^2$  present(?),  $pop^3$  absent(?).

ETYMOLOGY: Presumably from the Greek ἡμερος (hemeros), cultivated, and ῥίος (rhios),

(rhinos; masculine in accordance with item 30(a)(3) of the International Code of Zoological Nomenclature), nose.

DISTRIBUTION: Known from the type specimen, collected in deep water (69-91 meters) from Flores, Indonesia, and *H. opici* Blache and Bauchot (EA)\*.

REMARKS: Species of *Hemerorhinus* were unavailable for study. Blache and Bauchot's (1972) redescription of the type species clarified several confusing aspects of the original description, particularly in correcting the mistaken interpretation of the nostrils and fin position. From their discussion however, I am unable to confidently find its placement within this tribe. On the basis of Blache and Bauchot's illustrations, the cephalic pore condition would indicate a similarity to the species of *Yirrkala*.

#### *Ichthyapus* de Barneville

*Ichthyapus* de Barneville 1847: 219. (Type species; *I. acutirostris* de Barneville 1847, by monotypy.)

*Rhinenchelys* Blache and Bauchot 1972: 718. (Type species; *Sphagebranchus ophioneus* Evermann and Marsh 1902, by original designation.)

DESCRIPTION: Body elongate, cylindrical, pointed at both ends; tail longer than body; snout pointed, depressed, and broad dorsally, grooved and flattened on underside; lips without barbels; eye small; anterior nostril flush with snout, posterior opens into mouth; GO entirely ventral, with a thin medial membrane, converging forward, isthmus small; all fins absent;  $tp^2$  always and  $pop^4$  usually present; teeth pointed, uniserial, and largest at intermaxillary which are separated from those of vomer by a gap; skull depressed, broad, and truncate posteriorly (fig. 8); orbit extremely reduced; nasals moderately, and nasal cartilage well developed; SOC moderately projecting posteriorly; maxilla elongate and pointed posteriorly; suspensorium nearly vertical; opercular margins entire, preopercle reduced; hyomandibular broad, expanded anteriorly and posterodorsally; otic bulla moderately developed; PG elongate and rectangular posteriorly, with a slender projection from the anterodorsal corner; hyoid thickened (not as slender as in related genera); HH separated from CH by a narrow gap; branchiostegal rays not numerous, slender and generally unbranched, closely asso-

ciated with hyoid, outermost rays along EH broadened basally; UH cartilaginous for posterior two-thirds;  $C_5$  reduced (see Remarks),  $UP_3$ - $UP_4$  separate; CI broad, SCl usually absent, Sc and Co absent; posterior trunk parapophyses with an anterior marginal projection as in *Apterichtus* (fig. 33).

ETYMOLOGY: From the Greek *ἰχθύς* (ichthys), fish, and *ἄπτερος* (apous; masculine), without foot, presumably in reference to the lack of pectoral fins.

DISTRIBUTION: Circumtropical, with 6-7 valid species. Included are: *I. acutirostris* de Barneville (locality unknown)\*, *Sphagebranchus vulturis* Weber and de Beaufort (= *Caecula platyrhyncha* Gosline) (IP), *S. ophioneus* Evermann and Marsh (WA), *Apterichtus selachops* Jordan and Gilbert (EP), and three undescribed eastern and western Pacific forms. *Incertae sedis*: *Sphagebranchus omanensis* Norman (IP).

REMARKS: The sharp-snouted finless species previously placed in *Sphagebranchus*, excluding the species of *Cirricaecula* and *Apterichtus* as herein defined, are referred to *Ichthyapus*. The generic type, *I. acutirostris*, is obviously congeneric with those species according to descriptions of the type made by de Barneville (1847, fide Fowler, 1936: 293), Kaup (1856b: 29) and Blache and Bauchot (1972: 718-728).

Blache and Bauchot (1972) differentiated *Rhinenchelys* from *Ichthyapus* on the basis of minor differences in nostril condition and intermaxillary tooth location. My examination of the osteology of *ophioneus*, the type of *Rhinenchelys*, indicates that it is congeneric with *selachops*, *vulturis*, and presumably *acutirostris*.

Nelson (1966a: table 1, figure 19) has described and illustrated the gill arch condition of *I. vulturis* (as *Caecula platyrhyncha*). The fifth ceratobranchial ( $C_5$ ) is reduced and fused to the lower pharyngeal dermal tooth plate. I have found the gill arches of *I. ophioneus*, *I. vulturis*, and *I. selachops* to be similar in this condition. *Cirricaecula*, with a prominent  $C_5$ , appears intermediate between *Ichthyapus* and most Ophichthyini in this condition. The  $C_5$  condition of the related genus *Apterichtus*, based on my examination of *A. flavicaudus*, is the most reduced in the group.

#### *Lamnostoma* Kaup

*Lamnostoma* Kaup 1856: 49 (23). (Type species; *L. pictum* Kaup 1856 = *Dalophis orientalis*

McClelland 1844, by Jordan 1919b as first reviser.)

*Anguisurus* Kaup 1856: 50 (24). (Type species; *A. punctulatus* Kaup 1856 = *Dalophis orientalis* McClelland 1844, by monotypy.)

DESCRIPTION: Body stout, cylindrical, pointed at each end; body slightly longer than tail; snout pointed, its underside grooved; eye small to moderate; anterior nostril flush along snout, its posterior rim produced, posterior nostril usually associated with a pendulous flap; GO inferior, ca. equal to isthmus; DFO above or behind GO;  $tp^2$  and  $pop^3$  absent; teeth slender, pointed, and recurved, uniserial or biserial in jaws, those of intermaxillary and vomer largest and widely spaced; neurocranium truncate posteriorly, elongate and narrow, particularly along ethmoid and interorbital region; orbit depressed; nasals and nasal cartilage moderately developed; SOC present; maxillae moderately elongate, slender but not pointed posteriorly; coronoid process of articular greatly enlarged; opercular series moderately developed, their margins entire; suspensorium anteriorly inclined, jaw angle ca.  $100^\circ$ ; hyomandibular broad, expanded posterodorsally and strongly ridged; otic bulla well developed; PG slender, very reduced; hyoid slender, equal to branchiostegal rays in thickness, HH separated from CH by a broad gap, rays numerous, flat and unbranched, only the distal-most associated with hyoid, others terminate anteriorly behind tip of slender UH, outermost rays along EH slightly broadened; gill arches reduced,  $C_5$  absent,  $UP_3$ - $UP_4$  separate, B; cartilaginous except at anterior tip which is ossified; CI, SCl, and reduced Co and Sc present; coloration generally darker dorsally, a series of white spots across nape.

ETYMOLOGY: From the Greek *λαμίνα* (lamna), a horrible anthropophagous monster, a bugbear used by the Greeks to frighten refractory children (Jordan and Evermann, 1896: 49), and *στόμα* (stoma; neuter), mouth.

DISTRIBUTION: From the western Pacific, provisionally including four species.

REMARKS: *Lamnostoma* has been placed by recent authors in the synonymy of *Caecula*. It is herein found to differ markedly in numerous osteological and morphological characters, and is consequently resurrected. The species of this genus are generally collected in freshwater, and are easily recognized by their slender jaws and conspicuous white spotting on the head and

lateral line. Several nominal species are included in *Lamnostoma*, most of which fall into the synonymy of *L. orientalis* (McClelland). *Caecula mindora* Jordan and Richardson and *C. taylori* Herre are also referable to this genus. *Achirophichthys kampeni* (Weber and de Beaufort) is clearly a *Lamnostoma*. Its description, and recent references containing general morphological descriptions (Herre, 1924; Nichols, 1955; La Monte, 1961; Tortonese, 1964), concern large adults which have been collected in freshwater, each displaying the slender jaws and the head and body spotting of *Lamnostoma*.

*Stictorhinus* Böhlke and McCosker

*Stictorhinus* Böhlke and McCosker 1975: 5. (Type species; *S. potamius* Böhlke and McCosker 1975, by original designation.)

DESCRIPTION: General characteristics those of *Ichthyapus*. Differences include: Median fins present, low but distinct, DFO ca. mid-trunk; tp<sup>2</sup> present, pop<sup>4</sup> absent; LL ossicles with a short gap at pores; basisphenoid not elongate as in *Ichthyapus* (compare Figs. 8 and 9); SOC reduced; opercular series reduced, interopercle absent, preopercle reduced; branchiostegal rays numerous, branched basally in some individuals, closely associated with hyoid, outermost rays along EH broadened basally; UH a slender ossified filament posteriorly; C<sub>5</sub> absent; CI broad and expanded anteriorly, SCI absent, Sc and Co reduced; trunk parapophyses lack an anterior projection (fig. 33).

ETYMOLOGY: From the Greek *στικτός* (stiktos), pricked or punctured, and *ῥίς* (rhin, latinized to rhinus, nominative case), nose, in reference to the nature of the anterior nostrils.

DISTRIBUTION: A single western Atlantic species, known from tidal rivers in Brazil.

REMARKS: In 1971 Naercio Menezes sent the author a series of eels from freshwater in Brazil. These were identified as *Sphagebranchus rostratus* Bloch, a species known only from the type specimen said to have been from a "river in Surinam." Subsequent examination of the type specimens of *Caecula pterygera* and *Sphagebranchus rostratus* by J. E. Böhlke found them to be based on the same species, and the Brazilian specimens to be an undescribed genus and species (Böhlke and McCosker, 1975). My treatment (McCosker, 1973) of *Sphagebranchus* was therefore based on *Stictorhinus*.

*Yirrkala* Whitley

*Yirrkala* Whitley 1940: 410. (Type species; *Y. chaselingi* Whitley 1940 = *Sphagebranchus lumbricoides* Bleeker 1865, by original designation.)

*Pantonora* Smith 1964: 719. (Type species; *Ophichthys tenuis* Günther 1870, by original designation.)

DESCRIPTION: Body elongate, cylindrical, shorter than tail; snout conical, moderately developed, its underside grooved; eye moderate; anterior nostril in a short tube, posterior opens into mouth; GO ventral, longer than isthmus; DFO above or slightly behind GO; tp<sup>2</sup> usually present, pop<sup>3</sup> absent; teeth conical, pointed, nearly subequal, uniserial in jaws, those on vomer biserial anteriorly, separated from those of intermaxillary by a gap; skull not depressed, rounded posteriorly; orbit not strongly depressed; nasals and nasal cartilage moderately developed; SOC absent; maxilla pointed posteriorly; opercular series well developed, their margins entire; suspensorium anteriorly inclined, jaw angle ca. 100°; PG slender, pointed anteriorly; HH separated from CH by a short gap (HH absent in *Y. misolensis*); branchiostegal rays closely associated with hyoid; UH with a short projection posteriorly; C<sub>5</sub> absent, UP<sub>3</sub>-UP<sub>4</sub> separate; pectoral girdle contains SCI, CI, and reduced Co and Sc; posterior trunk parapophyses lack anterior marginal projections.

ETYMOLOGY: Named for *Yirrkala*, northern Australia, the type locality of the type species, masculine, in accordance with item 30(b)(ii) of the International Code of Zoological Nomenclature.

DISTRIBUTION: Contains approximately 12 species, from the eastern Atlantic, the Red Sea, and Indian and western Pacific Oceans. Included are: *Sphagebranchus lumbricoides* Bleeker, *Ophichthys tenuis* Günther, *Caecula maculata* Klauswitz, and an undescribed species from the Marquesas. *Incertae sedis*: *Sphagebranchus macrodon* Bleeker\*, *S. gjellerupi* Weber and de Beaufort\*, *S. kaupi* Bleeker, *Dalophis moluccensis* Bleeker\*, *Ophichthys misolensis* Günther, *Muraena lusca* Zuiew\*, and *Caecula natalensis* Fowler\*.

REMARKS: The description of *Yirrkala* is so lacking in diagnostic characters as to preclude its proper placement, and consequently has been ignored by most recent authors. The only subsequent reference to *Y. chaselingi*, the generic

type, which I have encountered is that of Munro (1957) in which this species is placed in *Sphagebranchus*. I have examined and x-rayed the badly damaged and dessicated paratype of *Y. chaselingi*. The anterior nostrils, head pores, and gill openings are too badly damaged to allow accurate examination, however the dentition is well preserved and agrees well with Whitley's illustration. In his description, Whitley stated that *Y. chaselingi* and *Sphagebranchus lumbricoides* are congeneric, differing in the "position of dorsal origin, proportion of head to trunk, in having vomerine teeth largest, and other details of proportions and dentition." My comparison of the paratype of *Y. chaselingi* and specimens of *S. lumbricoides* from Vietnam (CAS 13969) and the Philippines (CAS reg. 1607) indicates that they are conspecific. The proportions, dorsal fin origins, dentition, and vertebral numbers (*Y. chaselingi* = 153, *S. lumbricoides* = 151,154) are not different.

*Pantonora* Smith (1964) is herein considered a synonym of *Yirrkala*.

*Sphagebranchus kaupi* and *Ophichthys misolensis* are provisionally referred to *Yirrkala*. *Y. kaupi* differs in having the major axis of its GO vertical. *Y. misolensis* differs in having basihyals fused to the ceratohyals, lateral line ossicles consisting of numerous short coils rather than small block-like segments, and lacking  $tp^2$ .

The external morphology of the species of *Hemerorhinus*, as described by Blache and Bauchot (1972), indicates that those species might be conspecific with the species within this complex. A comparative study of the type species of *Yirrkala*, *Hemerorhinus*, and *Pantonora* is clearly needed.

#### Tribe Bascanichthyini

TYPE GENUS: *Bascanichthys* Jordan and Davis, 1892.

DIAGNOSIS: Body (head and trunk) and tail moderately to extremely elongate, generally cylindrical, and compressed posteriorly in some genera; body either equal to or longer than tail; lower jaw included; posterior nostril opens into mouth; GO low lateral, crescentic, never entirely ventral; median fins generally low, DFO on head in most genera; pectoral fin absent or present as a minute flap in upper GO corner; head pores reduced,  $pop^3$  and  $tp^2$  absent; LL ossicles nearly continuous or separated by a short gap at pores; teeth conical, not caniniform;

neurocranium variable in proportions and posterior shape; orbit generally reduced; otic bulla moderately to well developed; hyoid condition variable; branchiostegal rays numerous, associated with the hyoid; gill arches reduced,  $C_5$  absent in most genera; IM bones, ribs, and CTP developed; precaudal vertebrae generally more numerous than caudal; coloration nearly uniform, or darker posteriorly.

*Allips* McCosker

*Allips* McCosker 1972: 116. (Type species; *A. concolor* McCosker 1972, by original designation.)

DESCRIPTION: Body elongate, cylindrical for most of its length; body much longer than tail; head markedly rugose; snout blunt, its underside grooved; eye small; anterior nostril tubular; GO oblique, lateral, and less than isthmus in length; median fins low, DFO in anterior trunk region; pectoral minute; caudal blunt; tip of snout with numerous sensory hairs; LL ossicles nearly continuous; teeth small, conical, uniserial, intermaxillary teeth largest, separated from those of vomer; skull sloping posteriorly, orbit a narrow slit; SOC weakly developed; maxillae taper posteriorly; HH separated from CH by a gap; branchiostegal rays numerous, slender; pectoral girdle reduced, only CI, SCl, and a thin Co (?).

ETYMOLOGY: From the Greek  $\alpha\lambda\lambda\omicron\varsigma$  (allos), another, and  $\hat{\iota}\psi$  (ips; masculine), a worm.

DISTRIBUTION: A single species, known only from the type specimen from Thailand.

#### *Bascanichthys* Jordan and Davis

*Bascanichthys* Jordan and Davis 1891: 621. (Type species; *Caecula bascanium* Jordan 1885 = *Sphagebranchus teres* Goode and Bean 1882, by original designation.)

DESCRIPTION: Body elongate, cylindrical, and compressed posteriorly; body longer than tail; head markedly rugose; snout short and blunt, its underside grooved; mouth small; eye small; anterior nostril tubular; GO nearly horizontal, low lateral,  $\cong$  isthmus in length; median fins low, DFO on head; pectoral minute; caudal blunt; LL ossicles nearly continuous; teeth small, conical, uniserial in jaws, intermaxillary teeth separated from those of vomer by a short gap; neurocranium sloping posteriorly (fig. 10), orbit

reduced; nasals and nasal cartilage moderately developed, the nasals closely associated with the ethmoid for their entire length; SOC absent; maxilla weak, slender, and pointed posteriorly, attached before mid-vomer (fig. 16); opercular series moderately developed, their margins entire; suspensorium nearly vertical; otic bulla moderately developed; PG pointed anteriorly; HH separated from CH by a narrow suture; branchiostegal rays numerous, often branched basally, all along arch, the distal rays not broadened basally; UH either ossified or cartilaginous posteriorly;  $C_5$  reduced or absent,  $UP_3$ - $UP_4$  separate; pectoral girdle consists of reduced CI, SCI, Sc and Co.

ETYMOLOGY: From *Bascanion* (diminutive, from the Greek  $\beta\alpha\sigma\kappa\alpha\nu\acute{o}\varsigma$ , malignant), the generic name for the black snake, and  $\acute{\iota}\chi\theta\upsilon\varsigma$  (ichthys; masculine), fish.

DISTRIBUTION: All tropical oceans, with approximately 16 presently recognized species, including an undescribed eastern Pacific species from Cocos Island. Included are: *B. bascanoides* Osburn and Nichols (EP), *B. cylindricus* Meek and Hildebrand (EP), *B. panamensis* Meek and Hildebrand (EP), *B. ceciliae* Blache and Cadenat (EA)\*, *B. congoensis* Blache and Cadenat (EA)\*, *B. paulensis* Storey (WA), *B. pusillus* Seale (IP)\*, *Sphagebranchus teres* Goode and Bean (WA), *S. longipinnis* Kner and Steindachner (IP)\*, *S. scuticaris* Goode and Bean (WA)\*, *Callechelys myersi* Herre (IP), *Ophichthys filaria* Günther (IP)\*. *Incertae sedis*: *Callechelys longissimus* Cadenat and Marchal (EA)\*, and *Ophichthys kirkii* Gunther (IP)\*. *Leptenchelys tenuis* Tortonese, from New Guinea, is probably a junior synonym of *B. longipinnis*.

REMARKS: The species of *Bascanichthys* have been reviewed by Storey (1939), Ginsburg (1951) (western Atlantic), and Blache and Cadenat (1971) (eastern Atlantic). The status of *Bascanichthys pusillus*, considered a junior synonym of *B. filaria* by Fowler (1931: 316), is uncertain.

#### *Caralophia* Böhlke

*Caralophia* Böhlke 1955: 1. (Type species; *C. loxochila* Böhlke 1955, by original designation.)

DESCRIPTION: Body elongate, cylindrical, moderately compressed posteriorly; body longer than tail; snout subconical, blunt from above, lacking a groove on its underside; eye moderate; anterior nostril non-tubular, a hole with lateral projec-

tions into it; GO ventral, converging forward, longer than isthmus; median fins low, DFO on head; tail tip pointed; LL narrowly separated at pores; teeth bluntly conical, uniserial in jaws and on vomer, intermaxillary teeth slightly larger, separated from those of vomer by a short gap; skull sloping posteriorly, depressed dorsally, orbit reduced; nasals stout and well developed, their margins entire, tightly joined to ethmoid; nasal cartilage well developed; frontals extend posteriorly to mid-parietals; SOC moderately developed, SO extends from mid-frontals posteriorly to a strong point; maxilla weak, slender, and pointed posteriorly; opercular series developed, their margins entire; suspensorium posteriorly inclined, jaw angle ca.  $100^\circ$ ; otic bulla moderately developed; PG broad centrally, closely associated with maxilla anteriorly; hyoid stout, HH fused to CH; branchiostegal rays numerous, along arch, and often branched basally; distal rays along EH broadened basally; UH reduced to a well ossified basal plate with a posterior cartilaginous filament; tooth plates reduced,  $UP_3$ - $UP_4$  fused; pectoral girdle reduced to a CI and fragments of a SCI, Sc, and Co.

ETYMOLOGY: From the Greek  $\kappa\alpha\pi\alpha$ , head, and  $\lambda\omicron\phi\iota\alpha$  (lophia; feminine), a mane, in reference to the anterior dorsal fin origin.

DISTRIBUTION: A single western Atlantic species, extending from the Bahamas to the lesser Antilles and Panama.

#### *Dalophis* Rafinesque

*Dalophis* Rafinesque 1810a: 68. (Type species; *D. serpa* Rafinesque 1810a = *Sphagebranchus imberbis* De la Roche 1809.)

*Pterurus* Rafinesque 1810b: 59. (Type species; *P. illexosus* Rafinesque 1810b = *Sphagebranchus imberbis* De la Roche 1809, by monotypy.)

*Scytallurus* Duméril 1856: 199. (Type species; *Sphagebranchus imberbis* De la Roche 1809, by monotypy.)

*Pelia* Bleeker 1863: 128. (Type species; *P. cephalopeltis* Bleeker 1863.)

DESCRIPTION: Body moderately elongate, cylindrical, slightly compressed posteriorly; tail longer than body; snout sub-conical, grooved on underside; eye small; anterior nostril tubular; GO low on body, extending onto venter, its length  $\cong$  isthmus; vertical fins low, DFO well behind GO; pectoral fin rudimentary if present; tail tip blunt; LL ossicles widely separated at

pores; teeth conical, uniserial, intermaxillary teeth separated from those of vomer by a gap; skull subtruncate posteriorly, orbit depressed; nasals well developed; SOC weakly developed; maxilla tapers posteriorly; suspensorium nearly vertical; HH separated from CH by a gap; UH ossified posteriorly; gill arches stout, H<sub>3</sub> ossified, C<sub>5</sub> a slender ossified rod, UP<sub>3</sub>-UP<sub>4</sub> separate; pectoral girdle reduced, only a CI and SCl present.

ETYMOLOGY: The significance of the prefix is not obvious, but possibly derived from Dalmatia, then a country on the east side of the Adriatic Sea, and  $\delta\phi\lambda\varsigma$  (ophis; masculine), a snake.

DISTRIBUTION: Five eastern Atlantic and Mediterranean species are presently recognized, including: *D. bouleengeri* Blache and Bauchot (EA)\*, *D. multidentatus* Blache and Bauchot (EA)\*, *D. obtusirostris* Blache and Bauchot (EA)\*, *Pelia cephalopeltis* Bleeker (EA)\*, and *Sphagebranchus imberbis* De la Roche (M).

REMARKS: Blache and Bauchot (1972) have recently expanded *Dalophis* to include *Pelia* and five nominal species. Their finding (p. 746) that the pectoral fin, though generally absent, may be represented by a "miniscule filament" is in agreement with Lozano Rey's (1947, p. 546). Through the kindness of Enrico Tortonese I have been able to examine and partially dissect a specimen of *Dalophis imberbis*. A complete osteological preparation, however, was impossible.

*Dalophis* has been summarily synonymized with *Caecula* by previous authors. Its general facies (physiognomy, low median fins, and body depth and taper) and certain osteological features (dentition, pectoral girdle, and anterior trunk vertebrae) suggest a relationship with *Etheadophis* and *Leptenchelys*, genera restricted to the eastern Pacific. The gill arch skeleton and body/tail proportions are typically ophichthin, and for that reason, *Dalophis* is placed in the *Bascanichthyini* with reservations.

*Etheadophis* Rosenblatt and McCosker

*Etheadophis* Rosenblatt and McCosker 1970: 498. (Type species; *E. byrnei* Rosenblatt and McCosker 1970, by original designation.)

DESCRIPTION: Body moderately elongate, cylindrical anteriorly, becoming compressed posteriorly; body equal to or slightly longer than tail; snout rounded, conical from above; eye small; anterior nostril tubular; GO low on body,

extending onto venter, their length  $\cong$  to isthmus; vertical fins low, DFO before GO; tail tip blunt, fleshy in one species; LL ossicles separated at pores; teeth conical, uniserial, intermaxillary teeth separated from those of vomer by a gap; skull subtruncate posteriorly, orbit depressed; nasals well developed; SOC moderately developed, pointed as in *Bascanichthys*; maxilla tapers posteriorly; suspensorium nearly vertical; HH separated from CH by a gap; branchiostegal rays numerous, slender and along hyoid; UH ossified posteriorly; UP<sub>3</sub>-UP<sub>4</sub> separate; pectoral girdle reduced, only a CI, SCl, and Co (?) remnant visible by radiograph.

ETYMOLOGY: From the Greek  $\acute{\epsilon}\theta\alpha\varsigma$  (ethas), customary or ordinary, and  $\delta\phi\lambda\varsigma$  (ophis; masculine), serpent.

DISTRIBUTION: Two species, *E. byrnei* Rosenblatt and McCosker and *E. merenda* Rosenblatt and McCosker, known only from the type specimens from Baja California, Mexico.

#### *Gordiichthys* Jordan and Davis

*Gordiichthys* Jordan and Davis 1891: 644 (Type species; *G. irretitus* Jordan and Davis 1891, by original designation.)

DESCRIPTION: Body extremely elongate, cylindrical, much longer than tail; snout tapering; eye moderate; GO low lateral; DFO behind nape; teeth conical, recurved, and uniserial.

ETYMOLOGY: From *Gordius*, the horsehair worm, named after  $\Gamma\acute{o}\rho\delta\iota\omicron\varsigma$ , the king whose complicated knot was cut by Alexander, and  $\acute{\iota}\chi\theta\acute{\upsilon}\varsigma$  (ichthys; masculine), fish.

DISTRIBUTION: Known from a single deep-water western Atlantic species.

REMARKS: The above description is based on Jordan and Davis (1891) and Ginsburg (1951) in that material of *G. irretitus*, the type species, was unavailable for study. *Gordiichthys* will be redescribed by J. E. Böhlke (personal communication). *G. springeri* Ginsburg, its sole described congener, is a species of *Callechelys* (fide Rosenblatt and McCosker, 1970, and McCosker and Rosenblatt, 1972).

#### *Leptenchelys* Myers and Wade

*Leptenchelys* Myers and Wade 1941: 72. (Type species; *L. vermiformis* Myers and Wade 1941, by original designation.)



DESCRIPTION: Body elongate, cylindrical, slightly compressed posteriorly; body longer than tail; snout short, subconical; top of head and snout covered with numerous papillae; eye small; anterior nostril tubular; GO low lateral, crescentic,  $\cong$  isthmus; DFO on head; median fins confluent around tail tip; teeth weak, pointed, uniserial; skull sloping posteriorly, orbit reduced; SO rounded, not projecting posteriorly; suspensorium anteriorly inclined, jaw angle ca. 100°; hyoid arch slender, HH separated from CH by a narrow gap; branchiostegal rays slender, appear from radiograph to lie along hyoid; pectoral girdle reduced, only SCl and Cl visible in radiograph.

ETYMOLOGY: From the Greek λεπτός (leptos), thin, and ἐγχεύς (enchelys; either feminine or masculine, treated as masculine), eel.

DISTRIBUTION: A single species, known only from the type specimen from Playa Blanca, Pacific Costa Rica.

REMARKS: This poorly known genus is provisionally referred to the *Bascanichthyini*. The generic type, apparently uncollected since the capture of the 115 mm type specimen, was examined and radiographed for the purpose of this study. Its inclusion as a *bascanichthyin* is based on the numerous branchiostegal rays which appear to contact the hyoid, the posteriorly sloping neurocranium, the low unconstricted gill openings, and the head pore configuration. Caudal fin rays are present on the type specimen, but are more poorly developed than any *myrophine*'s.

*Leptenchelys* has had an erratic history. Originally placed in the *Echelidae* on the basis of its having a caudal fin (Myers and Wade, 1941), it was then synonymized with *Muraenichthys* by Schultz and Woods (1949), re-erected and expanded by Schultz, et al. (1953), and finally, restricted to a single species (McCosker, 1970) differing markedly from *Muraenichthys* and related genera. *Leptenchelys tenuis* Tortonese (1964) from New Guinea is a species of *Bascanichthys*, which is possibly synonymous with *B. longipinnis* described from Samoa. My examination of the holotype of *L. tenuis* indicates that Tortonese overlooked the rudimentary pectoral fin, similarly developed in *B. longipinnis* according to Storey (1939). The tail tip of *L. tenuis* is soft and fleshy, but not unlike that of other species of *Bascanichthys*.

*Phaenomonas* Myers and Wade

*Phaenomonas* Myers and Wade 1941: 77. (Type species; *P. pinnata* Myers and Wade 1941, by original designation.)

DESCRIPTION: Body elongate, cylindrical, much longer than tail; head markedly rugose; snout blunt, grooved ventrally; eye minute; anterior nostril tubular; GO low lateral, oblique and elongate,  $\cong$  isthmus; DFO mid-head, low, ending in anterior trunk region; anal fin absent; teeth small, conical, uniserial, intermaxillary teeth largest, separated from those of vomer; skull sloping posteriorly, orbital foramen a narrow slit; nasal cartilage weak; SOC weakly developed; maxilla tapers posteriorly; opercular series reduced, all but opercle serrated at margin; suspensorium anteriorly inclined, jaw angle ca. 100°; otic bulla well developed; PG free and tapering anteriorly; HH separated from CH by a gap; branchiostegal rays numerous, slender and along hyoid; UH club-shaped, cartilaginous posteriorly; pectoral girdle reduced, only SCl, Cl, and a thin Co (?); IM bones, ribs, and CTP weakly developed.

ETYMOLOGY: Presumably from the Greek φαίνω (phainos), to show, and μονάς (monas; feminine), single or alone, in reference to the unique dorsal fin condition.

DISTRIBUTION: Two described species, *P. pinnata* Myers and Wade ranging from the Gulf of California to Colombia, and *P. cooperae* Palmer, ranging from Hawaii to the western Indian Ocean (McCosker, In Press).

Tribe Ophichthini

TYPE GENUS: *Ophichthus* Ahl, 1789

DIAGNOSIS: Body (head and trunk) and tail moderately elongate, cylindrical anteriorly, generally compressed posteriorly; body usually shorter than tail; snout conical or subconical; lower jaw usually included; anterior nostril generally tubular; posterior nostril opens into mouth in most genera; gill openings lateral, their major axis vertical, crescentic, about equal to, less than, or longer than isthmus; median and pectoral fins present; tail tip sharply to bluntly pointed; tp<sup>2</sup> and pop<sup>4</sup> absent; dentition variable, including caniniform and molariform conditions; neurocranium moderately elongate; orbit well developed; otic bulla moderately to well developed; hyomandibular moderately to strongly ridged;

opercular series well developed, margins entire; gill arches well developed,  $C_5$  present in many genera; pectoral girdle generally well developed; intramuscular bones, ribs, and caudal transverse processes well developed; coloration variable.

#### *Aplatophis* Böhlke

*Aplatophis* Böhlke 1956b: 1. (Type species; *A. chauliodus* Böhlke 1956b, by original designation.)

DESCRIPTION: Body stout, not elongate, laterally compressed posteriorly; body slightly longer than tail; jaws elongate, the lower projecting beyond the upper; eye small; posterior nostril in a short tube before and beneath eye; GO vertical, lateral and elongate, less than isthmus; DFO behind pectoral tips; tail tip blunt;  $pop^3$  absent, median head pores absent although frontal commissure and supratemporal canal are present; LL ossicles widely separated at pores; anterior teeth of both jaws excessively developed as long fang-like canines extending far outside mouth when closed, jaw teeth biserial, those of vomer few and uniserial and continuous with those of intermaxillary; skull subtruncate posteriorly, orbit large, eyeball displaced anteriorly; PO ossicles weak, not fused as a strut to maxilla; nasals extremely reduced to a short and slender canal, nasal cartilage absent; frontal midline elevated anteriorly forming a sharp ridge extending to SO; SOC absent, SO anteriorly contacts frontals and separates parietals; maxilla elongate, rounded posteriorly; opercular series developed, subopercle scythe-shaped, preopercle enlarged; suspensorium posteriorly inclined, jaw angle ca.  $80^\circ$ ; hyomandibular ridged and elongate posterodorsally for muscle attachment; otic bulla well developed; PG broad posteriorly, free and terete anteriorly, HH separated from CH by a gap; branchiostegal rays slender, rays of EH joined basally; UH a spike posteriorly;  $C_5$  ossified,  $UP_3$ - $UP_4$  separate,  $B_{2-4}$  absent; pectoral fin moderately developed, girdle well developed, Sc and Co large, actinosts absent (fig. 19F); caudal vertebrae fewer than precaudal; coloration nearly uniform, slightly darker dorsally.

ETYMOLOGY: From the Greek ἀπλάτος (*aplatos*), unapproachable, and ὄφις (*ophis*; masculine), serpent.

DISTRIBUTION: Known from a single trans-Atlantic species.

#### *Brachysomophis* Kaup

*Brachysomophis* Kaup 1856: 45 (9). (Type species; *B. horridus* Kaup 1856 = *Ophisurus crocodilinus* Bennett 1833, by monotypy.)

DESCRIPTION: Body cylindrical, moderately elongate, longer than tail; snout very short, flat, blunt; jaws elongate, with lower jaw slightly protruding; eye moderate; a conspicuous transverse depression exists in the postorbital region of some species; lips with numerous small cirri; anterior nostril in a very short tube, posterior opens into mouth; GO low lateral, crescentic, longer than isthmus; DFO well behind pectoral tips; tail tip sharply pointed;  $pop^3$  absent; LL ossicles separated at pores; teeth strong, conical, maxillary biserial, dentary uniserial, those of vomer uniserial, large, and widely separated anteriorly but continuous with those of intermaxillary; skull subtruncate posteriorly, orbit reduced; dorsal-most postorbital with a broad anterior flange forming posterior margin of orbit, tightly sutured to smaller postorbitals to form a maxillary strut (fig. 15); nasals and nasal cartilage much reduced; SOC absent, SO broad posteriorly; maxilla elongate, tapering posteriorly; opercular series well developed, margins slightly serrate; suspensorium nearly vertical; hyomandibular ridged; otic bulla well developed; PG broad posteriorly, tapering to a fine point anteriorly; hyoid arch slender, HH separated from CH by a gap; branchiostegals slender and unbranched, closely associated with hyoid; UH a spike posteriorly;  $C_5$  ossified,  $UP_3$ - $UP_4$  separate; pectoral fin and girdle reduced, SCl and actinosts absent, SC reduced; caudal vertebrae fewer than precaudal; coloration uniform or darkened dorsally.

ETYMOLOGY: From the Greek βραχύς (*brachys*), short, σῶμα (*soma*), body, and ὄφις (*ophis*; masculine), serpent.

DISTRIBUTION: Known from four central and western Pacific and a single eastern Atlantic species. Günther's (1870) report of *B. crocodilinus* from the Galapagos Islands was probably erroneous (Rosenblatt et al., 1972).

REMARKS: The species of *Brachysomophis* are clearly in need of revision (Schultz, 1943; Smith, 1962) but I am lacking the material to make the required comparisons. *Brachysomophis atlanticus* Blache and Saldana (1972) was recently described from Senegal. The Pacific species of *Brachysomophis* include: *Ophisurus cirrhocheilos* Bleeker\*,

*O. corcodilinus* Bennett\*, *Brachysomophis henshawi* Jordan and Snyder, and *B. sauropsis* Schultz. The last three nominal species are quite similar and perhaps conspecific. *B. cirrhocheilos* differs from those species in apparently lacking the postorbital depression, in its longer pectoral fin, and faintly banded coloration (fide Deraniyagala, 1929). The neurocranium and suspensorium of *B. henshawi* were illustrated by Gosline (1951a: fig. 2).

The formation of the fused postorbital strut in species of *Brachysomophis* is functionally convergent with that of *Ophichthus zophochir*, however the third, dorsal-most postorbital of *B. sauropsis* is longer than the second, and enlarged anteriorly to form a cup that braces the eye.

*Cirrhimuraena* Kaup

*Cirrhimuraena* Kaup 1856; 51 (27). (Type species; *C. chinensis* Kaup 1856, by monotypy.)

*Jenkinsiella* Jordan and Evermann 1905: 83. (Type species; *Microdonophis macgregori* Jenkins 1903, by original designation.)

*Calamuraena* Whitley 1944: 261. (Type species; *Ophichthus calamus* Günther 1870, by original designation.)

*Calamuraena* Günther 1870, sic Rosenblatt and McCosker 1970: 496, lapsus pro *Calamuraena* Whitley 1944.

DESCRIPTION: General characteristics those of *Ophichthus*. Differences include: DFO generally on head or above GO; pectoral fin moderately to well developed; upper lip with numerous cirri; pop<sup>3</sup> generally present; teeth conical, pointed but not enlarged, often multiserial in jaws and on vomer, those of intermaxillary and vomer discontinuous; skull subtruncate posteriorly (more so than in *Ophichthus*); PO strut absent; SO and frontal crests weakly developed; maxilla elongate posteriorly; otic bulla not strongly developed; actinosts absent, or 1-2; coloration uniform, often darkened dorsally.

ETYMOLOGY: From the Latin *cirrus* (cirrh is a wrong but very common form of *cirr*, mistakenly considered to be from the Greek *κίρρος* [kirrhos] meaning yellow or tawny), *tendril*, and *Muraena*, a genus of muraenid eels.

DISTRIBUTION: An Indo-Pacific and Red Sea genus, with ca. 9 valid species.

REMARKS: *Cirrhimuraena* is broadly defined to include species that have been referred to *Calamuraena* and *Jenkinsiella*. Subgeneric lines within

*Cirrhimuraena* may be separated on an external morphological basis in the following manner:

- Mandibular and vomerine teeth uniserial;  
pop<sup>3</sup> absent (not determined for all species)  
..... subgenus *Jenkinsiella*
- Mandibular and vomerine teeth multiserial;  
pop<sup>3</sup> present (not determined for all species)  
..... subgenus *Cirrhimuraena*

The subgenus *Jenkinsiella* Jordan and Evermann includes *Microdonophis macgregori* Jenkins, *Ophichthus playfairii* Günther\*, and may include *Jenkinsiella oliveri* Seale\* and *J. inhacae* Smith\*. The remaining species belong in the subgenus *Cirrhimuraena* Kaup (which includes *Calamuraena* Whitley), including: *Cirrhimuraena chinensis* Kaup, *C. taeniopterus* Bleeker, *C. paucidens* Herre and Myers (= *C. chinensis*?), *Ophichthus calamus* Günther, and *Ophisurus cheilopogon* Bleeker\*. *Cirrhimuraena* may merit further generic division, particularly if confirmed by an osteological study of all the included species.

Nelson's (1966a: 395) description of the fifth ceratobranchial of *C. macgregori* as having "the proximal portion of C<sub>5</sub> cartilaginous . . . (and) the distal portion extending posteriorly as a thin filament of cartilage" does not agree with my findings on available specimens. In them the distal portion is well ossified. Gosline (1951a: fig. 6) has illustrated the neurocranium and suspensorium of *C. macgregori*.

*Echelus* Rafinesque

*Echelus* Rafinesque 1810a: 63. (Type species; *E. punctatus* Rafinesque 1810a = *Muraena myrus* Linnaeus 1758, by Bleeker 1864 as first reviser.)

*Myrus* Kaup 1856: 53 (31). (Type species; *M. vulgaris* Kaup 1856 = *Muraena myrus* Linnaeus 1758, by monotypy.)

DESCRIPTION: General characteristics those of *Ophichthus*. Differences include: DFO before pectoral tips; median fins continuous around tail; head pores reduced, pop<sup>3</sup> present, temporal, postorbital, and interorbital pores absent; cephalic surface sensory pores well developed; teeth multiserial, small, nearly granular, intermaxillary teeth continuous with those of vomer; PO strut absent, but a cartilaginous antorbital strut present in *E. myrus*; SO and frontal crests moderately developed; maxilla slender posteriorly; branchiostegal rays few; coloration nearly uniform, darker dorsally.

ETYMOLOGY: From the Greek  $\epsilon\chi\epsilon\lambda\upsilon\varsigma$  (enchelus, considered either feminine or masculine, regarded as masculine by Rafinesque, Kaup, and Bleeker), eel.

DISTRIBUTION: Known from a shallow and a deep-water species from the Mediterranean and eastern Atlantic, respectively, *E. myrus* (Linnaeus) and *Myrus pachyrhynchus* Vaillant.

REMARKS: The osteology of the species of *Echelus* indicates that they are closely related to species of *Ophichthus*, with particular similarities evidenced in the hyoid arches, gill arches, and neurocrania. The conspicuous presence of a caudal fin led previous workers to consider *Echelus* to belong to a family or subfamily separate from *Ophichthus*. The tail fin is clearly a superficial condition that does not merit such suprageneric separation, and thus the family name Echelidae is referred to the synonymy of the Ophichthidae, and the subfamily Echelinae to that of the Ophichthinae.

The species of *Echelus* are easily separable from other ophichthines on the basis of two characters, the presence of extremely visible caudal fin rays, and the head pore reduction. The produced caudal fin appears to be a primitive retention of an ancestral condition, although the hard-pointed tail tip characteristic of other ophichthines was probably achieved early in the evolution of the subfamily. The absence of the temporal, postorbital, and interorbital pores (as noted by Gosline, 1952) probably reflects the loss of these openings, in that the cephalic lateralis canals and frontal commissures of *E. myrus* (Allis, 1903: figs. 5-8, and personal observation) and *E. pachyrhynchus* (personal observation) have been retained. The antorbital cartilaginous strut of *E. myrus*, as identified by Gosline (1952), is not present in *E. pachyrhynchus* and does not appear to be an important indicator of phylogeny. Gosline (1952: 133) suggested that "*Echelus myrus* appears, despite specializations, to be by far the most primitive (or generalized) ophichthid known. In fact, to a considerable degree it fills in the gap between the Ophichthidae and the Congridae." I concur with Gosline in considering *Echelus* to be a very generalized (primitive) ophichthid, however its gill arch reduction, labial posterior nostril, and hyoid apparatus suggest that it is well separated from any congrid-like ancestor.

The neurocranium of *Echelus myrus* has been discussed and illustrated by Storms (1896, as

*Myrus vulgaris*) and by Gosline (1952), and the external morphology of *E. myrus* and *E. pachyrhynchus* by Blache (1968).

#### *Echiophis* Kaup

*Echiophis* Kaup 1856a: 46. (Type species; *Ophisurus intertinctus* Richardson 1844b, by monotypy.)

*Echiopsis* Kaup 1856b: 13. *Emend. pro Echiophis* Kaup 1856a.

*Crotalopsis* Kaup 1860: 12. Also spelled *Crotalopsis*, *Crotalophis*, by other authors. (Type species; *C. punctifer* Kaup 1860, by monotypy.)

*Macrodonophis* Poey 1867: 251. (Type species; *Conger mordax* Poey 1861, by monotypy.)

DESCRIPTION: Body cylindrical, moderately elongate, laterally compressed posteriorly; body shorter than tail; snout short, subconical, slightly constricted near tip; jaws elongate and subequal; eye moderate; posterior nostril in a short tube before and beneath eye; GO vertical, lateral and elongate,  $\cong$  ishtmus; DFO behind pectoral tips; tail tip blunt; pop<sup>3</sup> present; LL ossicles separated at pores; teeth strong, pointed and biserial, largest anteriorly in jaws and on ethmoid, those of intermaxillary and vomer biserial and nearly continuous; skull subtruncate posteriorly, preorbital region reduced, orbit large; PO fused to skull and maxilla, forming a strut; nasals slender, nasal cartilage reduced or absent; SOC absent; maxilla elongate, rounded posteriorly, toothed along most of its length; opercular margins entire, subopercle scythe-shaped; suspensorium posteriorly inclined, jaw angle ca. 85°; hyomandibular ridged and elongate posterodorsally for muscle attachment; otic bulla well developed; PG broad posteriorly, free and terete anteriorly; hyoid arch slender, HH separated from CH by a narrow gap; branchiostegal rays numerous, all slender, unbranched, and along hyoid; UH a spike posteriorly; C<sub>3</sub> ossified, UP<sub>3</sub>-UP<sub>4</sub> fused; pectoral girdle and fin developed, Sc and Co large, actinosts present; caudal vertebrae slightly more than precaudal; coloration generally strongly spotted.

ETYMOLOGY: From the Greek  $\epsilon\chi\iota\varsigma$  (echis), viper, and  $\omicron\phi\iota\varsigma$  (ophis; masculine), serpent. Kaup emended the suffix to  $\omicron\psi\iota\varsigma$  (opsis), appearance.

DISTRIBUTION: A largely New World genus containing 3-5 Atlantic and Pacific species. Included are: *Ophisurus intertinctus* Richardson (WA, and

EA as *Mystriophis cruetzbergi* Cadenat), *Conger mordax* Poey (WA), *Crotalopsis punctifer* Kaup (WA), and an undescribed eastern Pacific species ranging from the Northern Gulf of California to Panama. *Incertae sedis*: *Mystriophis blastorhinos* Kanazawa (WA).

REMARKS: The species of *Echiophis* form a distinctive complex within the Ophichthini, and are difficult to separate at the specific level. The Atlantic species are separable from each other on the basis of spot size, yet a continuous grade is clearly present. Opinions as to the distinctiveness of the Atlantic species have been presented (Jordan and Davis, 1891; Springer and Allen, 1932; Ginsburg, 1951) yet a conclusive study is still lacking. The morphology of eastern Atlantic specimens of *E. intertinctus* is described by Blache (1971).

#### *Elapsopsis* Kaup

*Elapsopsis* Kaup 1856: 45 (9). Emended to *Elapsopsis* by other authors. (Type species; *Ophisurus versicolor* Richardson 1844, by monotypy.)

*Cyclophichthys* Whitley 1951: 392. Described as a subgenus of *Malvoliophis* Whitley 1934. (Type species; *Ophichthus cyclorhinus* Fraser-Brunner 1934, by original designation.)

DESCRIPTION: General characteristics those of *Leiuranus*. Differences include: anterior nostril in a short tube, its rim flared distally; DFO above or slightly before GO; pectoral fin reduced,  $\cong$  GO length; vomerine teeth present; opercular margin fringed;  $C_5$  ossified; actinosts of pectoral girdle present.

ETYMOLOGY: From the Latin *elaps* (masculine), a snake, and *opsis*, an erroneous spelling of the Greek  $\delta\psi\upsilon\varsigma$  (opsis), meaning appearance.

DISTRIBUTION: Included are two, probably conspecific, species, from Australia, Lord Howe Island, and the southern Caroline Archipelago.

REMARKS: This genus is provisionally recognized as distinct from *Leiuranus* on the basis of the apparently secondary ossification of the fifth ceratobranchial and the presence of actinosts. The occasional presence of 1-2 vomerine teeth in specimens of *L. semicinctus* approaches the condition of certain specimens of *E. versicolor* and *E. cyclorhinus*. Further investigation may result in the recognition of *Elapsopsis* as a subgenus of *Leiuranus*.

#### *Evips* McCosker

*Evips* McCosker 1972: 113. (Type species; *E. per-cinctus* McCosker 1972, by original designation.)

DESCRIPTION: Body moderately elongate, cylindrical, laterally compressed posteriorly; body slightly longer than tail; snout blunt, conspicuously papillate; lower jaw included; eye large; DFO behind GO; pectoral fin minute; tail tip pointed;  $pop^3$  absent; LL ossicles continuous, but heavily fractionated; teeth pointed, uniserial, except those of maxilla which are biserial, largest at intermaxillary which are continuous with those of vomer; skull subtruncate posteriorly, orbit large; SOC pointed posteriorly; maxilla moderately produced, slender posteriorly; suspensorium nearly vertical, jaw angle ca.  $95^\circ$ ; hyoid stout, HH separated from CH by a gap; branchiostegal rays numerous, all slender and associated with hyoid; UH a spike posteriorly;  $C_5$  present,  $UP_3$ - $UP_4$  separate; pectoral girdle reduced to a slender CI (SCI not visible in radiograph), actinosts absent; caudal  $\cong$  precaudal vertebrae; coloration strong banded.

ETYMOLOGY: From the Greek  $\epsilon\upsilon$  (eu, latinized to ev for euphony before a vowel), good, and  $\iota\psi$  (ips; masculine), a worm.

DISTRIBUTION: A single species known only from the type specimen from the Southern Caroline Archipelago.

#### *Leiuranus* Bleeker

*Leiuranus* Bleeker 1853a: 24. (Type species; *L. lacepedii* Bleeker 1853a = *Ophisurus semicinctus* Lay and Bennett, by monotypy.)

*Stethopterus* Bleeker 1853a: 24. (Type species; *Ophisurus (Sphagebranchus) vimineus* Richardson 1844a = *Ophisurus semicinctus* Lay and Bennett 1839, by monotypy.)

*Machaerenchelys* Fowler 1937: 85. (Type species; *M. vanderbilti* Fowler 1937 = *Ophisurus semicinctus* Lay and Bennett 1839, by original designation.)

DESCRIPTION: Body moderately elongate, cylindrical, laterally compressed posteriorly; body and tail subequal; snout conical, flattened and grooved on underside; lower jaw included; eye moderate; anterior nostril in a short tube, posterior along lip margin; GO vertical, crescentic, shorter than isthmus; median fins low, expanded before tail tip; DFO above GO; pectoral fin moderately developed; tail tip sharply pointed;

pop<sup>3</sup> absent; LL ossicles narrowly separated at pores; teeth small, recurved, uniserial, absent from vomer or 1-2 small teeth; neurocranium subtruncate posteriorly, orbit large; PO strut absent; nasals and nasal cartilage moderately developed; frontal-parietal ridge and SOC developed; maxilla short, articulated ca. mid-vomer; maxillae closely apposed anteromedially (but not abutting as per Gosline, 1951a: 301); suspensorium anteriorly inclined, jaw angle ca. 100°; otic bulla well developed; PG slender, braced posteriorly by hyomandibular, pointed anteriorly; HH separated from CH by a short gap; branchiostegal rays numerous, slender (distal-most broadened slightly), unbranched, and associated with hyoid (except for innermost rays); UH split anteriorly (less so than in *Phyllophichthus*), produced posteriorly as a spike; gill arches weak, C<sub>5</sub> absent, anterior half of H<sub>1</sub> ossified; pectoral girdle reduced, actinosts absent; precaudal vertebrae more numerous than caudal; coloration strongly banded.

ETYMOLOGY: From the Greek  $\lambda\acute{\epsilon}\iota\omicron\varsigma$  (leios), smooth, and  $\omicron\upsilon\rho\alpha\nu\acute{\omicron}\varsigma$  (ouranos; masculine), sky, in reference to the toothless vomer.

DISTRIBUTION: A single species, widespread in the central and western Pacific and Indian oceans.

REMARKS: Gosline (1951a: fig. 4) has illustrated the neurocranium and suspensorium of *L. semicinctus*.

*Malvoliophis* Whitley

*Malvoliophis* Whitley 1934: 154. (Type species; *Bascanichthys hemizona* Ogilby = *Ophichthys pinguis* Günther 1872, by original designation.)

DESCRIPTION: Body elongate, subcylindrical, laterally compressed; body shorter than tail; snout developed, subconical, a short groove on underside; lower jaw included; eye large; anterior nostril tubular; DFO before GO; pectoral fin moderately developed; pop<sup>3</sup> absent; LL ossicles widely separated at pores; teeth conical, not sharply pointed, uniserial in jaws, largest at intermaxillary which are widely separated from those of the vomer; skull subtruncate posteriorly, orbit large; PO strut absent; maxilla elongate, slender posteriorly; opercular series weakly developed; suspensorium nearly vertical, jaw angle ca. 95°; otic bulla moderately developed; PG broad posteriorly, slender anteriorly; hyoid slender, HH separated from CH by a suture;

branchiostegal rays numerous, slender and slightly flattened, the anteriormost ray slightly enlarged; UH broad anteriorly, a short spike posteriorly; C<sub>5</sub> weakly ossified (cartilaginous?), UP<sub>3</sub>-UP<sub>4</sub> fused; pectoral girdle reduced, lacking Sc, Co, and actinosts; caudal vertebrae more numerous than precaudal; coloration weakly banded and spotted.

ETYMOLOGY: From Malvolio, Lady Olivia's steward in Shakespeare's *Twelfth Night*, and  $\omicron\phi\upsilon\varsigma$  (ophis; masculine), serpent. The banded coloration of *M. pinguis*, the generic type, suggests the cross-gartered legs and yellow socks worn by Malvolio (G. P. Whitley, personal communication).

DISTRIBUTION: A single species, reported from southern Queensland, New South Wales, and Lord Howe Island.

*Myrichthys* Girard

*Myrichthys* Girard 1859: 58. (Type species; *M. tigrinus* Girard 1859, by monotypy.)

*Chlevastes* Jordan and Snyder 1901: 867. (Type species; *Muraena colubrina* Boddaert 1781, by original designation.)

DESCRIPTION: General characteristics those of *Pisodonophis* and *Ophichthus*. Differences include: snout short (for an ophichthin), broad from above; DFO well before GO; pectoral fin short, broad-based (fig 34); pop<sup>3</sup> absent; teeth molariform or granular, multiserial on jaws and vomer, largest at intermaxillary, which are narrowly separated from those of vomer; PO strut absent; maxilla elongate, slender posteriorly; teeth of pharyngeal plates generally small and pavement like; pectoral girdle reduced, Co reduced, Sc and actinosts absent; coloration either spotted, banded, or both.

ETYMOLOGY: From the Greek  $\mu\acute{\upsilon}\rho\omicron\varsigma$  (myrus), eel, and  $\epsilon\chi\theta\upsilon\varsigma$  (ichthys; masculine), fish.

DISTRIBUTION: A circumtropical genus currently including seven valid species. The genus may be expanded to 12 should certain insular populations of *M. maculosus* and *M. xystrurus* prove to be distinct. Included in *Myrichthys* are: *M. bleekeri* Gosline (a substitute name for *Ophisurus fasciatus* var. *semicinctus* Bleeker, preoccupied) (IP), *M. sp.* (EP), *Muraena acuminata* Gronow (WA), *M. colubrina* Boddaert (IP), *M. maculosa* Cuvier (IP), *Pisodonophis oculatus* Kaup

(WA), *Ophisurus pardalis* Valenciennes (EA)\*, and *Ophichthys xystrurus* Jordan and Gilbert (EP) (see Remarks).

REMARKS: *Muraena tigrina* Rüppell (1826), described from the Red Sea, is currently placed in the synonymy of *Myrichthys maculosus* (Cuvier). This creates a homonymy with the eastern Pacific *Myrichthys tigrinus* Girard (1859), the type species of the genus. *Myrichthys xystrurus* (Jordan and Gilbert, 1882) is the next available name for the eastern Pacific species.

The genera *Pisodonophis* and *Myrichthys* are offshoots from a generalized *Ophichthus*-like ancestor. Within the examined species of *Pisodonophis* a trend in characters is evident, with *P. cancrivorus* the most *Ophichthus*-like and *P. daspilotus* the most *Myrichthys*-like (the characters however, are discontinuous enough to allow generic separation). These trends include: the transformation from pointed to molariform dentition; the advancement of the DFO; the reduction in length and basal broadening of the pectoral fin; and the reduction of the coracoid and loss of the scapula.

Harry (1949) has pointed out that the type locality of *M. tigrinus* is properly Adair Bay, Mexico, not Oregon.

Gosline (1951a) has illustrated the neurocranium, vertebrae, gill arches, and pectoral girdle of *M. maculosus*.

#### *Mystriophis* Kaup

*Mystriophis* Kaup 1856: 45 (10). (Type species; *Ophisurus rostellatus* Richardson 1844, by monotypy.)

DESCRIPTION: Body cylindrical, moderately elongate, laterally compressed posteriorly; body shorter than tail; snout short, subconical, constricted near tip; jaws elongate, the lower slightly inferior; eye moderate; posterior nostril at edge of upper lip, covered by a flap; GO vertical, lateral and elongate,  $\cong$  isthmus; DFO above or behind pectoral tips; tail tip blunt; pop<sup>3</sup> absent, secondary cephalic pores well developed; LL ossicles separated at pores; teeth strong, pointed, biserial, largest anteriorly in jaws and on ethmoid, intermaxillary and uniserial vomerine teeth nearly continuous; coloration nearly uniform, darkened dorsally.

ETYMOLOGY: From the Greek *μυστρίου* (mystrion), a spoon, and *ὄφις* (ophis; masculine), serpent, in relation to the snout shape of *M. rostellatus*, the generic type.

DISTRIBUTION: Two eastern Atlantic and one Japanese species are provisionally placed in *Mystriophis* (see following Remarks).

REMARKS: Specimens of *Mystriophis* were unavailable for osteological examination, therefore the above description was prepared from Blache (1971). The genera *Mystriophis* and *Echiophis* have been separated by recent authors (Ginsburg, 1951; Kanazawa, 1963; Rosenblatt and McCosker, 1970; Blache, 1971) on the basis of the snout shape and vomerine dentition. *M. rostellatus* Richardson and *M. crosnieri* Blache, from the eastern Atlantic, are undoubtedly congeneric and appear to be recently derived from an *Ophichthus*-like ancestor (evidenced in the pop<sup>3</sup> absence, secondary cephalic pore development, moderate snout length, and body coloration). The species of *Echiophis* however, appear to have been derived separately from a rather different *Ophichthus*-like ancestor (pop<sup>3</sup> present, secondary cephalic pores absent, shorter snout, and spotted coloration). *Ophisurus porphyreus* Temminck and Schlegel, from Japan, tentatively placed in *Brachysomophis* by Kanazawa (1963), probably belongs in *Mystriophis*. *M. blastorhinos* Kanazawa, from French Guiana, is either an *Echiophis* or belongs in a separate genus. Kanazawa's illustration of the pore pattern of *M. blastorhinos* is somewhat inaccurate; pop<sup>3</sup> and a single, rather than a double, interorbital pore are present (Kanazawa, in litt.).

#### *Ophichthus* Ahl

*Ophichthus* Ahl 1789: 5. Emended to *Ophichthus* by other authors. (Type species; *Muraena ophis* Linnaeus 1758, by original designation.)  
*Innominado* Parra 1781: 96. A junior synonym of *Muraena ophis* Linnaeus 1758, non-binomial.  
*Ophis* Turton 1807: 87. (Type species; "*O. maculata* . . . Spotted Serpent. Shaw Zool., iv. p. 22 . . . Bloch t. 154," presumably based on *Muraena ophis* Linnaeus 1758, by monotypy.)  
*Cogrus* Rafinesque 1810a: 62. (Type species; *C. maculatus* Rafinesque 1810a, by monotypy.)  
*Ophithorax* McClelland 1844: 212. (Type species; *Ophisurus ophis* Lacépède 1800, presumably based on *Muraena ophis* Linnaeus 1758, by Jordan, 1919b, as first reviser.)  
*Centrurophis* Kaup 1856: 42 (2). (Type species; *Ophisurus spadiceus* Richardson 1844, as a misidentification of *Ophichthys cephalazona* Bleeker 1864, by Jordan, 1919b, as first reviser.)  
*Poecilcephalus* Kaup 1856. 43 (5): (Type spe-

- cies; *P. bonaparti* Kaup 1856, by monotypy.)  
*Microdonophis* Kaup 1856: 43 (6). (Type species;  
*M. altipinnis* Kaup 1856, by monotypy.)  
*Coecilophis* Kaup 1856: 44 (6) (Type species;  
*Ophisurus compar* Richardson 1844 = *Ophisurus apicalis* Bennett 1830, by monotypy.)  
*Herpetoichthys* Kaup 1856: 44 (7). (Type species;  
*H. ornatissimus* Kaup 1856, by Jordan, 1919b,  
as first reviser.)  
*Muraenopsis* LeSueur, sic Kaup 1856: 46 (11),  
*lapsus pro Muraenophis* Lacépède 1825.  
*Scytalophis* Kaup 1856: 46 (13). (Type species; *S. magni-oculis* Kaup 1856, by Jordan, 1919b, as first reviser.)  
*Leptorhinophis* Kaup 1856: 46 (14). (Type species;  
*Ophisurus gomesi* Castelnau 1855, by Jordan, 1919b, as first reviser.)  
*Cryptopterus* Kaup 1860: 11. (Type species; *C. puncticeps* Kaup 1860, by monotypy.)  
*Uranichthys* Poey 1867: 256. (Type species; *Muraena hauannensis* Bloch and Schneider 1801 = *Muraena ophis* Linnaeus 1758, by Jordan and Davis, 1891, as first revisers.)  
*Oxydontichthys* Poey 1880: 254. (Type species;  
*Ophichthys macrurus* Poey 1880 = *Ophisurus gomesi* Castelnau 1855, by original designation.)  
*Omochelys* Fowler 1918: 3. Described as a subgenus of *Pisodonophis* Kaup. (Type species; *Pisodonophis cruentifer* Goode and Bean 1895, by original designation.)  
*Syletor* Jordan 1919a: 343. (Type species; *Pisodonophis cruentifer* Goode and Bean 1895, by original designation.)  
*Styletor* Jordan 1919a, sic Jordan, Evermann, and Clark 1930: 86, *lapsus pro Syletor* Jordan 1919a.  
*Acanthenchelys* Norman 1922: 296. (Type species; *A. spinicauda* Norman 1922, by original designation.)  
*Cryptopterenchelys* Fowler 1925: 1. Described as a subgenus of *Ophichthys* Ahl. (Type species; *Cryptopterus puncticeps* Kaup, as a substitute name for *Cryptopterus* Kaup 1860, preoccupied.)  
*Zonophichthys* Whitley 1930: 250. (Type species; *Ophichthys cephalazona* Bleeker 1864, by original designation.)  
*Gisenchelys* Fowler 1944: 188. Described as a subgenus of *Ophichthys* Ahl. (Type species; *Ophichthys zophochir* Jordan and Gilbert 1881, by original designation.)  
*Syletophis* Whitley 1950: 44. Substitute name for *Syletor* Jordan 1919a, preoccupied.

*Antobrancia* Ypiranga Pinto 1970: 13. (Type species; *A. ribeiroi* Ypiranga Pinto 1970 = *Muraena ophis* Linnaeus 1758, by original designation.)

DESCRIPTION: Body moderately to very elongate, laterally compressed posteriorly; body shorter than tail; snout moderately developed, subconical; lower jaw included; eye moderate to large; anterior nostril tubular, posterior along lower edge of lip or opening into mouth; DFO above or behind GO, but generally before pectoral tips; pectoral fin well developed; LL ossicles separated at pores; dentition variable, from numerous, small, and multiserial to few, large, and uniserial or biserial, never caniniform; teeth largest at intermaxillary and on vomer and sometimes separated by a short gap; skull subtruncate posteriorly (fig. 2), orbit large; PO strut developed in some species (fig. 14); nasals and nasal cartilage moderately developed; frontal and SO crests moderately to well developed; maxilla elongate, slender or rounded posteriorly (figs. 14, 16); opercular series well developed, their margins entire (fig. 14); suspensorium nearly vertical to posteriorly inclined; otic bulla well developed; PG broad posteriorly, free and terete anteriorly; hyoid slender, HH separated from CH by a narrow gap (fig. 17); branchiostegal rays slender, often numerous, unbranched and along arch; UH a spike posteriorly; gill arches complete, C<sub>5</sub> present, UP<sub>3</sub>-UP<sub>4</sub> separate (fig. 18); pectoral girdle well developed, actinosts present (fig. 19A); caudal vertebrae more numerous than precaudal; coloration generally uniform, although banded or spotted species may be included.

ETYMOLOGY: From the Greek ὄφις (ophis), snake, and ἰχθύς (ichthys, more correctly written ichthys; masculine), fish.

DISTRIBUTION: A circumtropical genus with approximately 55 species.

REMARKS: *Ophichthys* contains approximately 55 valid species, for which no fewer than 25 nominal genera have been erected. The genera *Gisenchelys* Fowler and *Zonophichthys* Whitley are here included in the synonymy of *Ophichthys*. Hubbs' (1932) inclusion of *Ophis* Turton in the synonymy of *Ophichthys* was neither included nor commented upon by Böhlke and Robins (1959) in their synonymy of *Ophichthys ophis*. Böhlke and Menezes (in litt.) have found *Antobrancia*, type species *A. ribeiroi* Ypiranga Pinto, to be an exact synonym of *Ophichthys ophis*.



The generic concepts of earlier authors, particularly Kaup, are nearly all based on differences in coloration or dentition. I have attempted to examine as many of these subgenera as possible. As broadly defined herein, *Ophichthus* exhibits a wide variety of morphological conditions, yet among the diverse types examined, I have found no accompanying differences that are clearly generic. It is particularly perplexing however, that the few osteological variations within the genus that might merit generic recognition are present in *O. triserialis*, *O. zophochir*, and the type species, *O. ophis*. These concern the development of the postorbital strut and the posterior shortening of the maxilla.

I have attempted to identify subgeneric lineages within *Ophichthus*, using available generic synonyms as subgeneric names. The following analysis however, must be regarded as strictly provisional:

Body  $\cong$  tail; DFO above or before GO; teeth minute and uniserial throughout; coloration of several species strongly spotted)....

..... subgenus *Microdonophis* Kaup

Body shorter than tail; DFO behind GO, generally above pectoral tips; teeth larger, often multiserial .....

Anterior nostril a broad tube, flared at tip; intermaxillary block hooked downward, and intermaxillary teeth directed horizontally backward; tail tip hard and sharply-pointed; median fins conspicuously expanded before tail tip .....

..... subgenus *Centrurophis* Kaup

Anterior nostril tubular, not flared distally; intermaxillary teeth erect, with tips hooked back; tail tip hard and blunt, not sharply-pointed; median fins conspicuously expanded before tail tip .....

.....subgenus *Centrurophis* Kaup

Postorbital bones tightly sutured and bracing maxilla, forming a strut; maxilla rounded posteriorly; jaw and vomerine dentition bi- or triserial .....

.....subgenus *Ophichthus* Ahl

Postorbital bones not tightly sutured and not forming a strut with maxilla; maxilla elongate and slender posteriorly; dentition variable, either uniserial or multiserial .....

..... subgenus *Coecilophis* Kaup

Included in the subgenus *Microdonophis* are: *M. altipinnis* Kaup (IP), *M. erabo* Jordan and

Snyder (IP), *Ophichthus polyophthalmus* Bleeker (IP)\*, and *O. melanochir* Bleeker (IP).

Included in the subgenus *Centrurophis* are the generic types of *Zonophichthus* and probably *Poecilcephalus*. Included species: *Ophichthus cephalazona* Bleeker (IP), and *Poecilcephalus bonaparti* Kaup (IP)\*.

Included in the subgenus *Ophichthus* are the generic types of *Innominado*, *Ophis*, *Cogrus*, *Uranichthys*, *Ophithorax*, and *Gisenchelys*. Included species: *Muraena ophis* Linnaeus (WA, EA), *Muraenopsis triserialis* Kaup (EP), and *Ophichthys zophochir* Jordan and Gilbert (EP). A complete synonymy of *O. ophis* is provided by Böhlke and Robins (1959).

Included in the subgenus *Coecilophis* is *Ophisurus apicalis* Bennett (IP), and presumably many other species listed below as *incertae sedis*.

*Incertae sedis*: *Acanthenchelys spinicauda* Regan (WA)\*, *Cogrus maculatus* Rafinesque (M)\*, *Conger urolophus* Schlegel (IP), *Cryptopterus puncticeps* Kaup (WA), *Echelus rufus* Rafinesque (M)\*, *Omochelys marginatus* Fowler (WA) (= *Ophichthus cruentifer* ?), *Ophichthus asakusae* Jordan and Snyder (IP), *O. manilensis* Herre (IP)\*, *O. melanoporus* Kanazawa (WA), *O. multiserialis* Norman (IP)\*, *O. retifer* Fowler (IP)\*, *O. roseus* Tanaka (IP)\*, *O. stenopterus* Cope (IP)\*, *Ophichthys ascensionis* Studer (WA)\*, *O. ater* Peters (EP)\*, *O. callensis* Günther (EP), *O. derbeyensis* Whitley (IP)\*, *O. episcopus* Macleay (IP)\*, *O. evermanni* Jordan and Snyder (IP), *O. frontalis* Garman (EP), *O. garretti* Günther (IP)\*, *O. limkouensis* Chen (IP)\*, *O. macrops* Günther (IP)\*, *O. madagascariensis* Fourmanoir (IP)\*, *O. melanochir* Bleeker (IP), *O. pacifici* Günther (EP), *O. retropinnis* Eigenmann (WA)\*, *O. unicolor* Regan (IP)\*, *O. woosuitingi* Chen (IP)\*, *Ophisurus celebicus* Bleeker (IP)\*, *O. gomesii* Castelnau (WA), *O. grandoculis* Cantor (IP)\*, *O. macrochir* Bleeker (IP), *O. marginatus* Peters (IP)\*, *O. parilis* Richardson (WA)\*, *O. reguis* Richardson (EA)\*, *O. remiger* Valenciennes (probably EP, no type locality given)\*, *O. rutidoderma* Bleeker (emended by most authors to *rhytioderma*), (IP)\*, *O. rutidodermatoides* Bleeker (emended by most authors to *rhytiodermatoides*), (IP), *Pisodonophis cruentifer* Goode and Bean (WA), *Scytalophis magnioculis* Kaup (WA)\*, and two undescribed Eastern Pacific species.

*Ophisurus* Lacépède

*Ophisurus* Lacépède 1800: 195. (Type species; *Muraena serpens* Linnaeus 1758, as restricted

by Risso 1826.)

*Leptognathus* Swainson 1838: 334. (Type species; *L. oxyrhynchus* Swainson 1838 = *Muraena serpens* Linnaeus 1758, by original designation.)

*Leptorhynchus* Smith 1847: 244. (Type species; *L. capensis* Smith 1847 = *Muraena serpens* Linnaeus 1758.)

*Anepistomon* Gistel 1848: ix. A substitute name for *Leptorhynchus* Smith 1847, preoccupied.

DESCRIPTION: General characteristics those of *Ophichthus*. Differences include: body very elongate; snout attenuate, jaws elongate, slender, incapable of closing completely in adults; lower jaw included; anterior nostril lateral, at mid-snout (fig. 24B), posterior on outer lip and covered by a flap; DFO beyond tips of pectoral fins; cephalic surface sensory papillae well developed (figs. 24B, C); teeth conical, nearly uniserial, enlarged along vomer; maxilla elongate, slender and produced posteriorly; coloration uniform, darker dorsally.

ETYMOLOGY: From the Greek *ὄφις* (ophis), serpent, and *οὐρά* (oura), tail, and *-ος* (-us), masculine suffix.

DISTRIBUTION: Presumably a single species, known from the Mediterranean, eastern Atlantic, Cape of Good Hope, the western and central Indian Ocean, eastern Australia, New Zealand, and Japan. *Ophisurus macrorhynchus* Bleeker 1852, from Japan, differs slightly in morphometry from the Mediterranean *Muraena serpens*, yet a conclusive comparison has not been made.

REMARKS: The Atlantic and Pacific populations of *O. serpens*, if indeed conspecific, represent the most disjunct of known ophichthid distributions. Historically, the Mediterranean population could be explained as a relict of a Tethyan species. Parallels may be found in the disjunct populations of other eel species (see D. Smith, 1969), such as *Kaupichthys diodontus*, which presumably ranges from the western Atlantic, and the central and western Pacific, and Indian oceans (J. L. B. Smith, 1965), and *Dysomma anguillare*, presumably ranging from the tropical western Atlantic, Indian Ocean, and off Japan and China (Robins and Robins, 1970).

The identity of *Ophichthus multiserialis* Norman 1939 from the Gulf of Aden, included by J. L. B. Smith (1962: 455) in *Ophisurus*, has not been determined.

*Oxystomus Rafinesque* (1810b: 62) has been considered by most authors to be synonymous with *Ophisurus*. Castle (1969) however, has con-

firmed Bertin's (1935) suggestion that the type species, *Oxystomus hyalinus*, is based on a post-metamorphic *Serrivomer* rather than a larval *Ophisurus serpens*.

The external morphology and osteology of *Ophisurus serpens* (as *O. novaezealandiae* Hector) was described by Knox (1870).

#### *Phyllophichthus* Gosline

*Phyllophichthus* Gosline 1951a: 316. (Type species; *P. xenodontus* Gosline 1951a, by original designation.)

DESCRIPTION: Body moderately elongate, cylindrical, laterally compressed posteriorly; body  $\cong$  tail; snout produced, subconical, grooved on underside; lower jaw included; eye large; anterior nostril subtubular, its posterior borders extending downward into leaflike appendages, posterior nostril opens into mouth; GO vertical, crescentic, shorter than isthmus; dorsal and anal fins low, expanded before the sharply pointed tail tip; DFO above GO; pectoral fin well developed; pop<sup>3</sup> absent; LL canal ossicles are short coils separated at pores; teeth conical, minute, and uniserial in jaws, curved on mandible, absent from vomer; neurocranium elongate, subtruncate posteriorly, orbit large; PO strut absent; nasals and nasal cartilage well developed; SOC absent; maxilla fragile and not produced, articulated ca. mid-vomer (fig. 16); preopercle reduced; suspensorium anteriorly inclined, jaw angle ca. 100°; otic bulla moderately developed; PG slender, short, and pointed anteriorly; hyoid slender, HH absent, CH with a minute anterior condyle (possibly a remnant of a fused HH?); branchiostegal rays numerous, filamentous, free from hyoid; UH split anteriorly, produced posteriorly as a slender spike; gill arches weak, pharyngeal teeth minute, C<sub>s</sub> absent, H<sub>1</sub> ossified only at tip; pectoral girdle well developed, actinosts present; precaudal vertebrae more numerous than caudal; coloration uniform.

ETYMOLOGY: From the Greek *φύλλον* (phylon), leaf, and *Ophichthus* (masculine), a genus of ophichthids, in reference to the leaf-like anterior nostrils.

DISTRIBUTION: Two described Pacific species, *P. xenodontus* Gosline from the central and western Pacific and Indian oceans, and *P. macrurus* McKay\*, described from Australia.

#### *Pisodonophis* Kaup

*Pisodonophis* Kaup 1856a: 47. Also spelt *Piso-*

*dontophis* by other authors. (Type species; *Ophisurus cancrivorus* Richardson 1844, as restricted by Bleeker 1865.)

*Pisodonophis* Kaup 1856b: 17. *Emend. pro Pisodonophis* Kaup 1856a.

*Brachycheirophis* Fowler 1944: 190. (Type species; *Pisodonophis daspilotos* Gilbert, in Jordan and Evermann 1898, by original designation.)

DESCRIPTION: General characteristics those of *Ophichthus*. Differences include: pectoral fin broad-based; pop<sup>3</sup> present or absent; teeth molariform or granular, multiserial on jaws and vomer, largest at intermaxillary with a short gap separating those of the vomerine block; PO strut absent; maxilla elongate, slender posteriorly; innermost branchiostegal rays free from hyoid; teeth of pharyngeal plates generally small, pavement-like; pectoral girdle reduced, actinosts absent, Sc absent in one species; coloration generally uniform, spotted in one species.

ETYMOLOGY: From the Greek  $\pi\acute{\iota}\sigma\omicron\varsigma$  (píσos), pea,  $\omicron\delta\omicron\nu\varsigma$  (odons), tooth, and  $\omicron\phi\iota\varsigma$  (ophis; masculine), serpent.

DISTRIBUTION: Known from 8-10 species, a circumtropical genus. Included are: *Ophisurus cancrivorus* Richardson (IP), *O. boro* Hamilton-Buchanan (IP), *O. hijala* Hamilton-Buchanan (IP)\*, *O. hoevenii* Bleeker (IP), *O. hypselopterus* Bleeker (IP)\*, *O. semicinctus* Richardson (EA)\*, *Pisodonophis copelandi* Herre (IP), *P. daspilotos* Gilbert (EP), *Pisodonophis zophistus* Jordan and Snyder (IP) (= *P. cancrivorus*?), *Ophichthus dromicus* Günther (EA)\*.

REMARKS: The relationships of *Pisodonophis*, *Myrichthys*, and their *Ophichthus*-like ancestors are discussed in the remarks on *Myrichthys*.

*Omocheilus* Fowler, considered by recent authors to be a junior synonym of *Pisodonophis*, is here referred to *Ophichthus*. *Omocheilus cruentifer* is unlike the species of *Pisodonophis* in having few branchiostegal rays, all of which are attached to the hyoid.

Ganguly and Nag (1964) described the functional morphology of the pectoral girdle and the acranial myomeric musculature of a fish they identified as *Ophichthus boro*. The pectoral girdle they have crudely illustrated is clearly not that of *Pisodonophis boro*, and is probably from a species of *Ophichthus*. Tilak and Kanji (1967) noted their error and properly described the morphology of the pectoral girdle of *Pisodono-*

*phis boro* in relation to its habit.

#### *Pogonophis* Myers and Wade

*Pogonophis* Myers and Wade 1941: 78. (Type species; *P. fossatus* Myers and Wade 1941, by original designation.)

DESCRIPTION: Body moderately elongate, cylindrical, laterally compressed posteriorly; body slightly longer than tail; snout blunt; jaws subequal, a single pendulous barbel on upper lip; eye large; anterior nostril tubular, with a posterior tag; DFO behind GO; pectoral fin minute; tail tip pointed; preopercular pores vertically, not obliquely aligned, pop<sup>3</sup> absent; LL ossicles nearly continuous; teeth pointed, uniserial except on maxillae where biserial, largest at intermaxillary which is continuous with those of vomer; skull subtruncate posteriorly, orbit large; PO strut absent; nasals and nasal cartilage reduced; SOC weakly pointed; maxilla elongate, slender posteriorly; suspensorium posteriorly inclined, jaw angle ca. 80°; otic bulla moderately developed; PG broad posteriorly, free and terete anteriorly; hyoid slender; HH separated from CH by a broad gap; branchiostegal rays numerous, all slender and associated with hyoid, the anteriormost 3-4 rays fused basally; UH broad anteriorly, short and slender posteriorly; gill arches reduced, C<sub>3</sub> absent, UP<sub>3</sub>-UP<sub>4</sub> separate; pectoral girdle weakly developed, actinosts absent; caudal ≡ precaudal vertebrae; coloration strongly spotted.

ETYMOLOGY: From the Greek  $\pi\omega\gamma\omega\nu$  (pogon), beard, and  $\omicron\phi\iota\varsigma$  (ophis; masculine), serpent, in reference to the conspicuous barbel on the snout.

DISTRIBUTION: A single eastern Pacific species, ranging from the Gulf of California to Peru (as *Ophichthus afuerae* Hildebrand).

#### *Quassiremus* Jordan and Davis

*Quassiremus* Jordan and Davis 1891: 622. (Type species; *Ophichthus evionthas* Jordan and Bollman 1889, by original designation.)

DESCRIPTION: Body moderately elongate, cylindrical, laterally compressed posteriorly; body slightly longer than tail; snout developed, conical, a short groove on underside; lower jaw included; eye large; DFO behind GO; pectoral fin minute; tail tip pointed; pop<sup>3</sup> present; LL ossicles continuous; teeth pointed, uniserial, largest at intermaxillary and continuous with those

of vomer; skull truncate posteriorly, orbit large; PO strut absent; nasals well developed, nasal cartilage weakly developed; SOC strongly pointed; maxilla elongate, slender posteriorly; opercular margins entire; suspensorium anteriorly inclined, jaw angle ca. 100°; otic bulla well developed; PG broad posteriorly, free and terete anteriorly; hyoid slender, HH separated from CH by a broad gap; branchiostegal rays numerous, all slender and associated with hyoid, the anteriormost 3-4 rays fused basally; UH broad anteriorly, short and slender posteriorly; gill arches reduced, C<sub>5</sub> absent, UP<sub>3</sub>-UP<sub>4</sub> separate; pectoral girdle reduced to a slender CI and SCl; caudal = precaudal vertebrae; coloration strongly spotted.

ETYMOLOGY: From the Latin *quassus*, obliterated, and *ramus* (masculine), oar, in reference to the minute pectoral fins.

DISTRIBUTION: Known from 3 New World species. Included are: *Ophichthus evionthas* Jordan and Bollman (EP), *Ophichthus nothochir* Gilbert (EP) (including *Q. parvipinna* Seale), and *Quasiremus productus* Seale (WA) (including *Q. goslingi* Beebe and Tee-Van).

REMARKS: The osteological description of *Quasiremus* is based on *Q. nothochir*. *Q. evionthas*, the generic type, was examined from radiographs and gill arch dissection.

#### *Scytalichthys* Jordan and Davis

*Scytalichthys* Jordan and Davis 1891: 635. Described as a subgenus of *Mystriophis* Kaup. (Type species; *Ophichthus miurus* Jordan and Gilbert 1882, by original designation.)

DESCRIPTION: Body cylindrical, moderately elongate, longer than tail; snout very short, flat, subconical; jaws elongate, lower jaw inferior; eye moderate; anterior nostril in a short tube, posterior opens into mouth; GO low lateral, crescentic, longer than isthmus; DFO well behind pectoral tips; pectoral fin reduced; tail tip bare, sharply pointed; pop<sup>3</sup> absent; LL ossicles continuous, not separated at pores; teeth strong, conical, those on maxilla in two widely separated rows, uniserial on dentary; those on vomer large, uniserial, widely separated, and continuous with those on intermaxillary; skull subtruncate posteriorly, orbit reduced; PO not bracing maxilla; nasals very reduced, nasal cartilage reduced; SOC absent, a short broad posterior projection; maxilla elongate, bifurcate posteriorly, the distal

section elongate and terete, the medial shorter and pointed; opercular series well developed, their margins entire; suspensorium nearly vertical, hyomandibular strongly ridged; otic bulla well developed; PG slender, a fine point anteriorly; hyoid arch slender, HH widely separated from CH; branchiostegal rays numerous, all slender, unbranched, and along arch; UH a short spike posteriorly; C<sub>5</sub> short, UP<sub>3</sub>-UP<sub>4</sub> nearly fused, lower pharyngeal plate elongate; pectoral girdle reduced, SCl and actinosts absent; IM bones, ribs, and CTP well developed; caudal vertebrae fewer than precaudal; coloration strongly spotted.

ETYMOLOGY: From the Greek *σκυτάλη* (skytale), viper, and *ἰχθύς* (ichthys; masculine), fish.

DISTRIBUTION: A single eastern Pacific species, ranging from the Galapagos Islands to the Gulf of California and Guadalupe Island.

REMARKS: Schultz (1942) has commented on the generic status of *Scytalichthys* with regard to its dentition.

#### *Xyrias* Jordan and Snyder

*Xyrias* Jordan and Snyder 1901: 864. (Type species; *X. revulsus* Jordan and Snyder 1901, by original designation.)

DESCRIPTION: Body cylindrical, moderately elongate, longer than tail; snout short, subconical; jaws elongate, the lower inferior; eye moderate; anterior nostril non-tubular, laterally ovate, with a minute ventral flap; posterior nostril outside mouth and covered with a flap; GO low lateral, crescentic, longer than isthmus; DFO behind pectoral tips; pectoral fin moderate; tail tip bare, pointed; pop<sup>3</sup> absent; teeth strong, conical, not extremely enlarged; those of vomer largest, uniserial, and nearly continuous with those of intermaxillary, jaw teeth multiserial; orbit depressed; PO not bracing maxilla; nasals and nasal cartilage reduced; SOC with a short posterior projection; maxilla elongate, bifurcate posteriorly; opercular series well developed, their margins entire; suspensorium nearly vertical; PG slender, tapering to a fine point anteriorly; hyoid arch moderately slender, HH separated from CH by a gap; branchiostegals numerous, slender, unbranched and along arch; C<sub>5</sub> ossified, UP<sub>3</sub>-UP<sub>4</sub> united by a suture; pectoral girdle complete, SCl, CI, Sc, Co, and actinosts visible in radiograph; IM bones, ribs, and CTP well developed; caudal vertebrae fewer than precaudal; coloration of numerous small spots.

ETYMOLOGY: From the Greek *ῥυπίας* (masculine), a shaveling, in reference to the absence of cirri on the lips.

DISTRIBUTION: A single species from Japan. Glover (1973) reported that it is caught occasionally by shrimp trawlers in the Misaki, Kochi, and Kumano prefectures.

REMARKS: This description was prepared from radiographs and a gill arch dissection of the holotype.

#### *Comparison with Previous Classifications*

The results of the present study offer certain insights into the reliability of superficial morphological characters as a basis for classification. The most recent attempt at a compilation of genera within the Ophichthidae was that of Rosenblatt and McCosker (1970). That study was based on an analysis of previous literature and an examination of all recognized genera except *Neenchelys*, *Malvoliophis*, and *Benthenchelys* (Castle, 1972, was the first to suggest that *Benthenchelys* is an ophichthid). The following discrepancies exist between the results of that study and the present:

(a) *Echelus* was included in the Myrophinae (as Echelinae), following Gosline (1952); in the present study *Echelus* is shown to be an ophichthine, and the presence of a caudal fin is not regarded as a definitive character separating the ophichthid subfamilies;

(b) *Leptenchelys* was included in the Myrophinae, again based on the caudal condition; in the present study it is suggested that its relationships lie with the Bascanichthyini;

(c) *Lamnostoma* was considered to be synonymous with *Caecula*; in the present study osteological characters have been identified that allow its generic separation;

(d) *Omochelys* was considered to be synonymous with *Pisodonophis* on the basis of tooth characters; in the present study it is indicated that its affinities lie closer to species of *Ophichthus* than of *Pisodonophis*, and *Omochelys* is tentatively placed in the synonymy of *Ophichthus* awaiting a revision of that large and cumbersome genus;

(e) *Jenkinsiella*, and *Microdonophis* and *Zonophichthus*, were recognized at the generic level; in the present study no osteological characters have been found to support their generic recognition, and they are reduced to subgeneric rank under *Cirrhimuraena* and *Ophichthus*, respec-

tively.

The results of this comparison however, have shown that the previous classification, based for the most part on external morphological characters, was not seriously upset by a classification based primarily on osteology. The finding of greatest consequence was that the affinities of *Echelus* lie with the Ophichthinae rather than the Myrophinae; the caudal fin condition was shown to be trivial when compared with the "Ophichthus-like" condition of numerous osteological characters.

In that the majority of classification schemes within the teleosts are now based on external morphological characters, it is somewhat reassuring to realize that at least within the Ophichthidae, the external morphological classification parallels that based on osteology.

## EVOLUTION OF THE OPHICHTHIDAE

### *Relationship to other Anguilliforms*

Recent authors have summarily recognized 23 families within the suborder Anguilloidei (Greenwood, et al., 1966; Gosline, 1971). Subsequent studies have changed this listing in the following manner. Robins and Robins (1970) have expanded the Dysommidae to include the Dysommidae and the Nettodaridae and (1971) provisionally united the Nessorhamphidae with the Derichthyidae. Smith (1971) has provisionally removed *Coloconger* from the Congridae and erected the family Colocongridae. The above-mentioned authors have allocated the anguilloid families to five superfamilies, namely: the Anguilloidea (those eel families with paired frontals), Synaphobranchoidea (Synaphobranchidae, Dysommidae and Simenchelyidae), Congroidea (Congridae, Colocongridae, Muraenesocidae, Nettastomidae, and Macrocephenchelyidae), Nemichthyoidea, and Ophichthoidea.

The superfamily Ophichthoidea is restricted to the Ophichthidae. They appear most closely related to the superfamily Congroidea, but differ in the condition of several major characters (several fundamental characteristics of the Ophichthidae and related apodal families are indicated in Table 7). As Smith (1971) has shown, the congroids possess a complete pterygoid arch and a nearly complete gill arch skeleton. Conversely, the ophichthid pterygoid is reduced and well separated from the vomer, and their gill arches exhibit various stages of reduction. The ophichthids also differ from the congroids in possessing

numerous and overlapping branchiostegal rays, a fused frontal commissure, and a cartilaginous connection between the first epibranchial and second infrapharyngobranchial of the gill arch skeleton. Certain congrid, primarily within the subfamily Heterocongrinae, are similar to ophichthids in the development of laminar ribs, reduced neural spines, an elongate body, and a fleshy tail tip (cf. Böhlke, 1957; Rosenblatt, 1967). Rosenblatt discussed these similarities and suggested (p. 95) that "the superficial similarities between *Gorgasia* and the ophichthids are certainly parallel adaptations to a similar mode of life, and the minor osteological similarities may be adaptations as well."

The general condition of the primitive ophichthid genera, viz., *Echelus* and *Ophichthus*, appears to be derived from a congrid ancestor. To my knowledge, no known congrid exhibits definitive ophichthid characters in an intermediate state of development, particularly the fused frontal commissure and overlapping branchiostegal rays. The achievement of the ophichthid condition may have been a quantum jump in apodal evolution, attained by either an advanced congrid or congrid ancestor by means of a rapid integration of the above mentioned characters. Yet this may only be presumed until further evidence from extant or fossilized species is obtained.

#### Evolution within the Ophichthidae

The purposes of any classification system are to best reflect the phylogenetic history of the taxa involved and to provide predictability, such that a newly discovered taxon might be properly placed without upsetting the system. An evolutionary scheme may only be inferred from existing data, and must carefully weigh the probabilities related to each hypothetical pathway. In dealing with supra-specific categories, one is faced with the difficulty of delineating groups on a subjective basis. The history of the Ophichthidae, however, would suggest that the genus, tribe, and subfamily reflect certain biological realities in an evolutionary sense. The present study has attempted to define and identify these groupings. The presence of several fundamental osteological characters in both major lines of the Ophichthidae suggests a monophyletic origin of the family. These characters include the frontal commissure, the epibranchial interconnections, and the unique manner of branchiostegal overlap. The two subfamilies differ trenchantly in the manner in which the branchiostegal rays are attached to the hyoid, yet this difference need not preclude a monophyletic origin. The inferred subfamilial and tribal evolution within the Ophichthidae is illustrated below in Figure 37. Generic evolution within each tribe is treated in the following discussion.

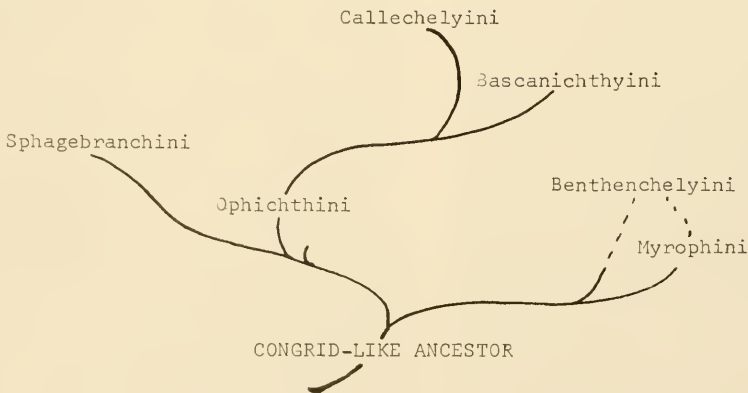


Figure 37. Proposed evolutionary relationship of ophichthid tribes.

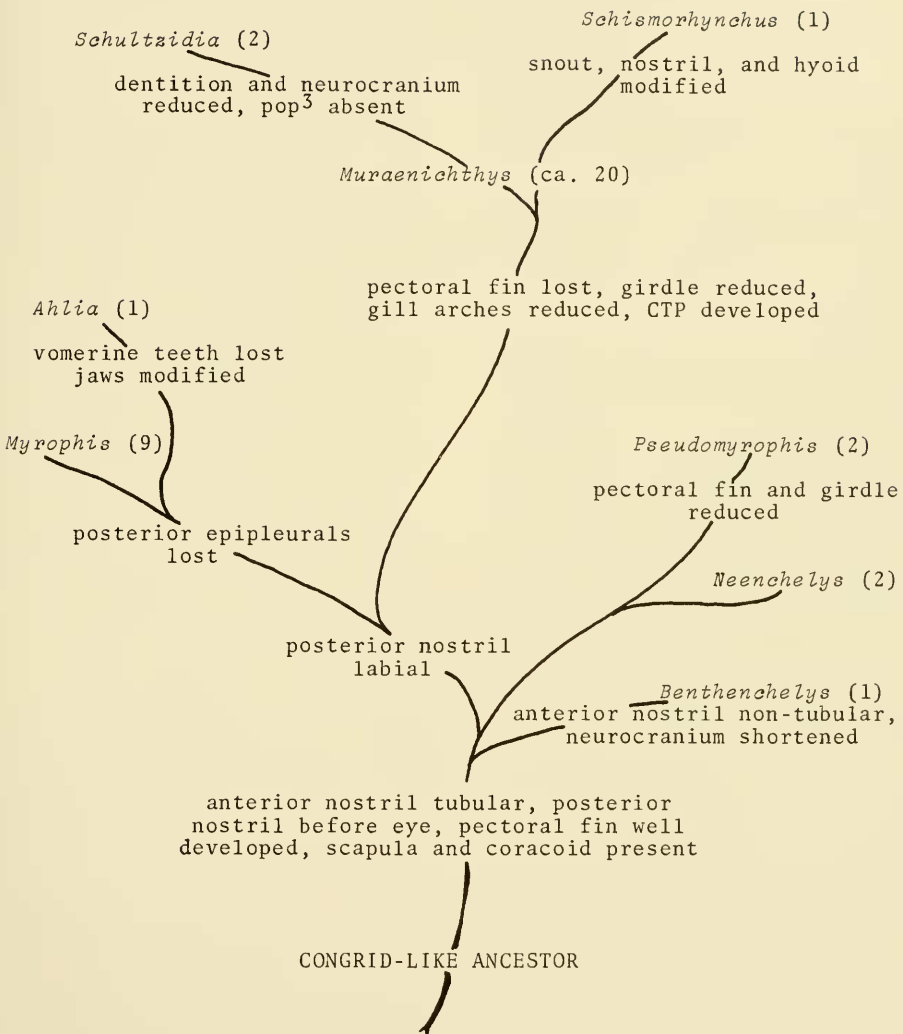


Figure 38. Proposed evolution of the Myrophinae. Number of species in parentheses.

*Myrophini* and *Benthenchelyini*. Two conditions indicate that the Myrophinae probably arose from the first dichotomy of the ophichthid lineage (Figs. 37-38). These are the presence of a well developed caudal fin and the unique myrophine branchiostegal condition in which the majority of the rays are free from and well behind the epihyal. The attached rays, like those of the congrid, are basally broadened. Although the species of *Echelus* possess a myrophine-like caudal fin, they also possess an ophichthine-like hyoid and other osteological conditions that link them with the Ophichthinae.

Primitive conditions of certain characters within the Myrophinae include:

- (a) teeth present on the dentary, intermaxillary, maxilla, and vomer;
- (b) pectoral fin moderately to well developed;
- (c) coracoid and scapula present;
- (d) posterior nostril lateral;
- (e) first basibranchial ossified;
- (f) seven attached branchiostegals along epihyal;
- (g) anterior nostril tubular;
- (h) eye not enlarged, its diameter ten or more in head length.

*Benthenchelys cartieri*, the single species within the Benthenchelyini, is highly specialized for its unique adaptation to a pelagic existence (see Remarks on *Benthenchelys*). It has however, retained certain primitive conditions which would suggest that it separated early from the ancestral myrophine stock. *Benthenchelys* possess all the primitive conditions listed above except that its first basibranchial has been reduced to cartilage. Whether *Benthenchelys* separated before, after, or along with the *Neeenchelys-Pseudomyrophis* lineage was not discerned from the available data. The posterior nostril of *Neeenchelys* and *Pseudomyrophis*, like that of *Benthenchelys*, is lateral. The nostril of *Benthenchelys* is extremely atypical within the Ophichthidae in that it is markedly more dorsally located than it is in other genera. The partial re-ossification of the third hypobranchial in *Benthenchelys* probably represents a secondary specialization; the third hypobranchial of all congrid, and presumably that of the basal ophichthids, is cartilaginous.

Similarities between *Neeenchelys* and *Pseudomyrophis* were described earlier in this study. These genera have retained the first basibranchial, the pectoral fin, and pectoral girdle, but an attached branchiostegal has been lost in two of

the three species examined. *Pseudomyrophis* has become specialized in the reduction of its pectoral fin and girdle, and in one species the body has become extremely elongate. *Neeenchelys* is somewhat more primitive in that it has retained a developed pectoral fin and its girdle is not reduced.

Beyond the level of the *Pseudomyrophis-Neeenchelys* separation, the posterior nostril has become labial in position. In general, the ophichthid posterior nostril lies within the mouth or along the lip and is covered by a flap. The reversion to the more generalized and presumably primitive condition in which the posterior nostril lies along the outer edge of the lip has been achieved numerous times. This is evidenced in the contrasting posterior nostril conditions of closely related genera such as *Ichthyapus* and *Apterichtus*, *Ophichthus* and *Ophisurus*, and particularly between the species of *Muraenichthys*. A distinction however, should be made between the condition of the earlier-removed myrophine genera (*Benthenchelys*, *Pseudomyrophis*, and *Neeenchelys*) and that of the remaining ophichthids. In no case does it appear that the posterior nostril has secondarily returned to a congrid-like placement.

The next major dichotomy is that of the *Ahlia-Myrophis* lineage. That they arose from a common ancestor is evidenced by their conspicuous specialization in which the pleural ribs are limited to the anterior trunk vertebrae. The species of *Myrophis* differ considerably in external appearance, primarily in body and snout elongation, even though they differ little osteologically. *Ahlia egmontis*, by comparison, is specialized in having lost the vomerine dentition, posteriorly shortened maxillae, modified pterygoids, the hypohyals either lost or fused to the ceratohyal, and the dorsal fin origin withdrawn to the level of the anus.

The remainder of the Myrophini comprise the species of *Muraenichthys*, *Schultzidia*, and *Schismorhynchus*, commonly called the "worm eels". The reductions and specializations of the latter two genera must preclude them as ancestors to *Muraenichthys* or to each other. Within *Muraenichthys* however, are species sufficiently generalized that either *Schismorhynchus* or *Schultzidia* might have been derived from them. As discussed in the remarks on *Muraenichthys*, subgeneric lineages, although including rather divergent extremes, are bridged by a broad spectrum of morphological conditions. The more gen-



eralized species of the subgenus *Scolecenchelys* are likely ancestors to the subgenus *Muraenichthys* and the genera *Schultzidia* and *Schismorhynchus*. Species of *Scolecenchelys* have the posterior nostril within the mouth, separate upper pharyngeal tooth plates, an ungrooved snout, uniserial or biserial conical teeth, and a third preopercular pore (pop<sup>3</sup>). Species of the subgenus *Muraenichthys* have an external posterior nostril, multiserial granular dentition, a deep body, a blunt snout, and fused upper pharyngeal teeth. The species of *Schultzidia* have lost the pop<sup>3</sup> and the dentition is extremely reduced, being absent on the vomer, absent or embedded on the intermaxillary, and minute or villiform in the jaws. *Schismorhynchus labialis* is specialized in quite a different manner, and seems to have been derived from a *Muraenichthys*-lineage different from that of *Schultzidia*. It is an elongate worm eel that has undergone specializations apparently related to its mode of feeding. A prominent toothed groove divides the underside of the snout and extends anteriorly to the elongate tubular nostrils. The suspensorium is forwardly inclined, and although the dentition is generalized, the upper pharyngeal tooth plates are fused, and certain gill arch members (H<sub>3</sub> and I<sub>2</sub>) are absent.

*Ophichthini*. The Ophichthini include the most primitive and generalized of ophichthids. Primitive conditions of certain characters include:

- (a) caudal rays developed;
- (b) pectoral, dorsal, and anal fins well developed;
- (c) branchiostegal rays fewer than 20;
- (d) teeth conical, often multiserial, present on maxilla, dentary, vomer, and intermaxillary;
- (e) fifth ceratobranchial (C<sub>5</sub>) ossified as a slender rod, upper pharyngeal tooth plates separate;
- (f) third preopercular pore (pop<sup>3</sup>) present;
- (g) neurocranium truncate posteriorly;
- (h) tail approximately 60 percent of the total length.

The species of *Echelus* possess all of the above characters and represent one branch of the ophichthine lineage (Fig. 39). All subsequent ophichthines are specialized in having the tail tip reduced to a finless point. Although differences exist in the condition of the tail tip, in no instance are caudal rays developed as in *Echelus* or the myrophines. The genus *Ophichthus*, as broadly defined herein, is the most generalized of the remaining ophichthine genera, having

character states that embrace most of the variation of the other genera. The changes in other genera have to do with the loss or specialization of characters, or rearrangements of the basic *Ophichthus* condition. Certain lineages within *Ophichthus* appear ancestral to lineages within the tribe itself. For example, those species with few branchiostegal rays and an average body taper probably gave rise to the long-jawed piscivorous genera. The proposed sphaegebranchin lineage can also be derived from generalized ophichthine characters.

*Ophisurus* appears to be an offshoot from a moderately elongate *Ophichthus*-like species with few branchiostegals, nearly uniform dentition, and well developed surface sensory papillae. Its jaws and neurocranium modifications merit its generic recognition.

The species of *Quassiremus* share several primitive characters with *Ophichthus*, but have become specialized through the reduction of the pectoral fin and loss of the C<sub>5</sub> and pectoral girdle elements.

The species of *Pisodonophis*, *Myrichthys*, and *Cirrhimuraena* probably arose from a common lineage, evidenced in their increased number of branchiostegals and generally multiserial dentition. *Cirrhimuraena* is specialized in the development of labial cirri. Differences between the species of *Cirrhimuraena* are probably deserving of subgeneric rank, as discussed in the remarks on this genus. *Pisodonophis* and *Myrichthys* share several unique similarities, primarily their multiserial molariform dentition and broad-based pectoral fins. *Myrichthys* is further specialized in the loss of pop<sup>3</sup>, the reduction of the pectoral fin and girdle, and the advancement of the DFO. As mentioned in the remarks on *Myrichthys*, a nearly continuous character series exists from species of *Ophichthus* → *Pisodonophis* → *Myrichthys*.

The species of *Mystriophis*, *Echiophis*, *Brachysomophis*, *Aplatophis*, *Xyrias*, and *Scytalichthys* form a natural group of predaceous ophichthines specialized for the capture of large struggling prey. These specializations include the development of a postorbital strut to brace the maxilla, the strengthening of the suspensorium, enlargement of the vomerine and jaw dentition, the advancement and dorsal location of the eyes on the snout, and the attainment of a large size as adults. Certain species of *Ophichthus* (*O. ophis*, *O. triserialis*, and *O. zophochir*) are similarly specialized. The character states of *Echiophis*

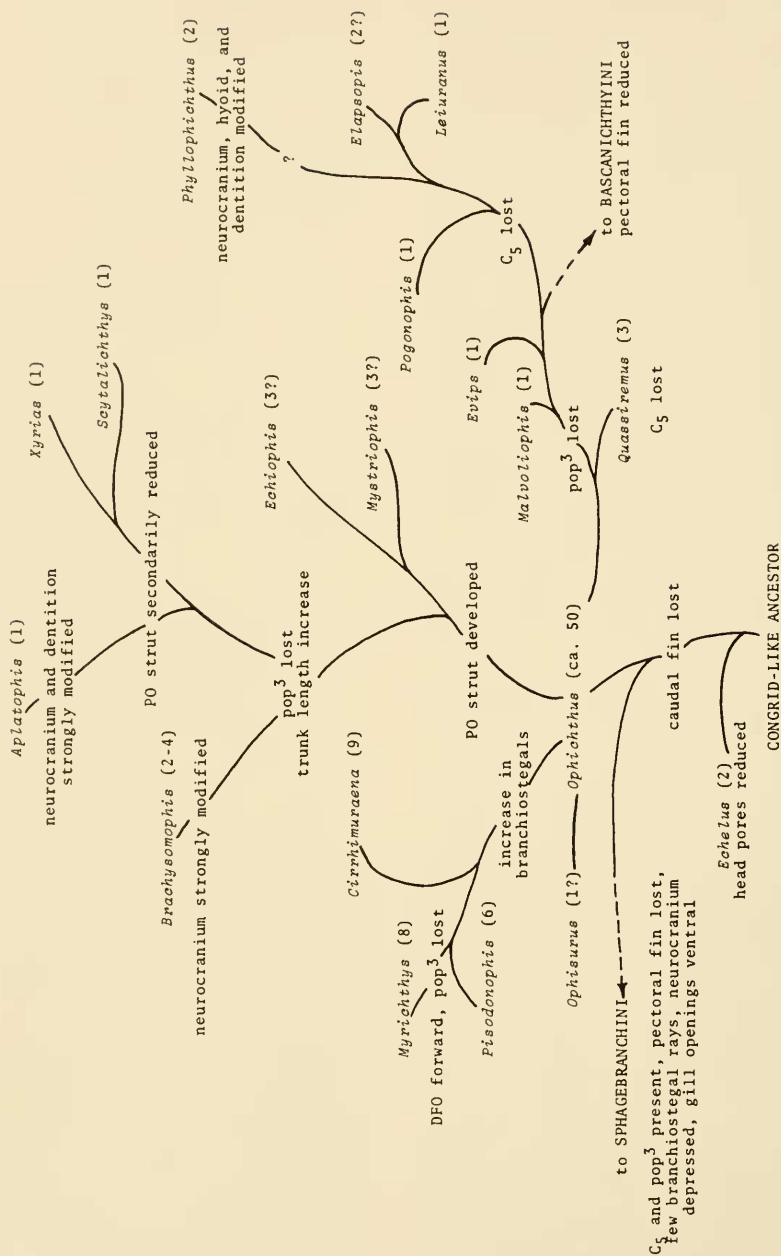


Figure 39. Proposed evolution of the Ophichthini.

and *Mystriophis* are merely further specializations of the condition of those species of *Ophichthus*. As mentioned in the remarks on *Mystriophis*, the specializations of *E. blastorhinos*, when further investigated, may merit generic recognition. Remaining genera in the lineage are further specialized by having a proportionately longer trunk region, or conversely, a shorter tail, and have lost the  $pop^3$ . The examined species of *Brachysomophis* have developed labial cirri and a massive postorbital strut. The translocation of the orbit to the snout tip and development of the surface sensory papillae system in *Brachysomophis* and *Scytalichthys* correlate with the feeding behavior; these species, like those of *Echiophis* (personal observation, and Hiatt and Strasburg, 1960), lie within their burrows with only their snout tips exposed, awaiting the passage of prey items. The advantages of the eye position and papillae development are obvious. A similar feeding behavior is practiced by other ophichthines. Species of *Callechelys*, for example, have been observed (personal observation) and R. H. Rosenblatt, (personal communication) with the head protruding from the sand bottom, apparently awaiting the passage of prey items. *Callechelys* has not undergone the development of the strengthened suspensorium and elongated jaws and associated orbit translocation typical of the long-jawed ophichthines, and feeds primarily on relatively smaller and weaker prey. The development of labial cirri in *Brachysomophis* and other ophichthine genera probably serves as a screen to prevent fine sediment from entering the mouth. The absence of the postorbital strut in the remaining genera is assumed to be a secondary reduction. *Xyrias* and *Scytalichthys* are quite similar in the shape of their maxillae and in the condition of their multiserial dentition. *Scytalichthys* has a proportionately longer trunk region and has a further modified snout condition. *Aplatophis* is conditionally placed at the apex of this lineage. Its numerous reductions and specializations make its placement within the lineage difficult.

The remaining ophichthine genera have lost the  $pop^3$ . *Malvoliophis* has diverged from the *Ophichthus* condition in having an advanced DFO. *Evips* has retained an *Ophichthus*-like DFO, but has a considerably reduced pectoral fin and girdle and a proportionately reduced tail length. The ancestral bascanichthyin probably arose from this lineage, and probably possessed an anterior DFO, an ossified  $C_5$ , and a reduced pectoral fin

and girdle. Subsequent ophichthines have lost the rod-like ossified  $C_5$  possessed by all other ophichthines. *Pogonophis*, although similar in external appearance to species of *Ophichthus*, is specialized in its development of labial barbels and by its loss of the  $C_5$  and  $pop^3$ . *Leiuranus* and *Elapsoepis* are closely-related genera which have departed from *Ophichthus* in snout shape,  $UP_3$ - $UP_4$  fusion, and reduced pectoral fins and girdles; *Leiuranus* is further specialized in the loss of vomerine dentition and certain pectoral elements. *Phyllophichthus* is aligned with this lineage although its exact placement is undetermined. Its suspensorium, jaws, dentition, and neurocranium are extremely modified.

*Sphagebranchini*. The Sphagebranchini comprise a specialized ophichthin offshoot of highly modified species, assembled on the basis of the absence of the pectoral fin, pectoral girdle reductions, and low or entirely ventral gill openings. Primitive conditions of certain characters include:

- (a) neurocranium depressed;
- (b) branchiostegal rays fewer than 20;
- (c)  $pop^3$  and  $tp^2$  pores present;
- (d)  $C_5$  ossified;
- (e) dorsal and anal fins present;
- (f) anterior nostrils tubular, posterior nostrils within mouth;
- (g) body and tail nearly subequal;
- (h) gill openings low lateral.

The interpretation of intergeneric relationships within this tribe is made difficult by the reduction or loss of numerous characters. Several interpretations are possible, depending upon the importance applied to certain characters. The following interpretation, in assuming the tribe to have had a monophyletic origin, assumes that the  $C_5$  has been lost independently in two lineages. This loss seems plausible through an ossified  $\rightarrow$  cartilaginous transformation, and has apparently occurred elsewhere in the family.

The preliminary dichotomy separates the three sharp-snouted, entirely finless genera (Fig. 40). Each possesses a peculiar projection from the parapophyses of the anterior trunk vertebrae (Fig. 33A), a specialization not observed elsewhere in the tribe. *Cirricaecula* is primitive in having retained an *Ophichthus*-like  $C_5$  but specialized in its  $UP_3$ - $UP_4$  fusion, entirely ventral non-converging gill openings, and labial cirri development. The species of *Ichthyapus* have a small eye, reduced anterior nostril, and cartilaginous  $C_5$ . Species of *Apterichtus* have entirely lost

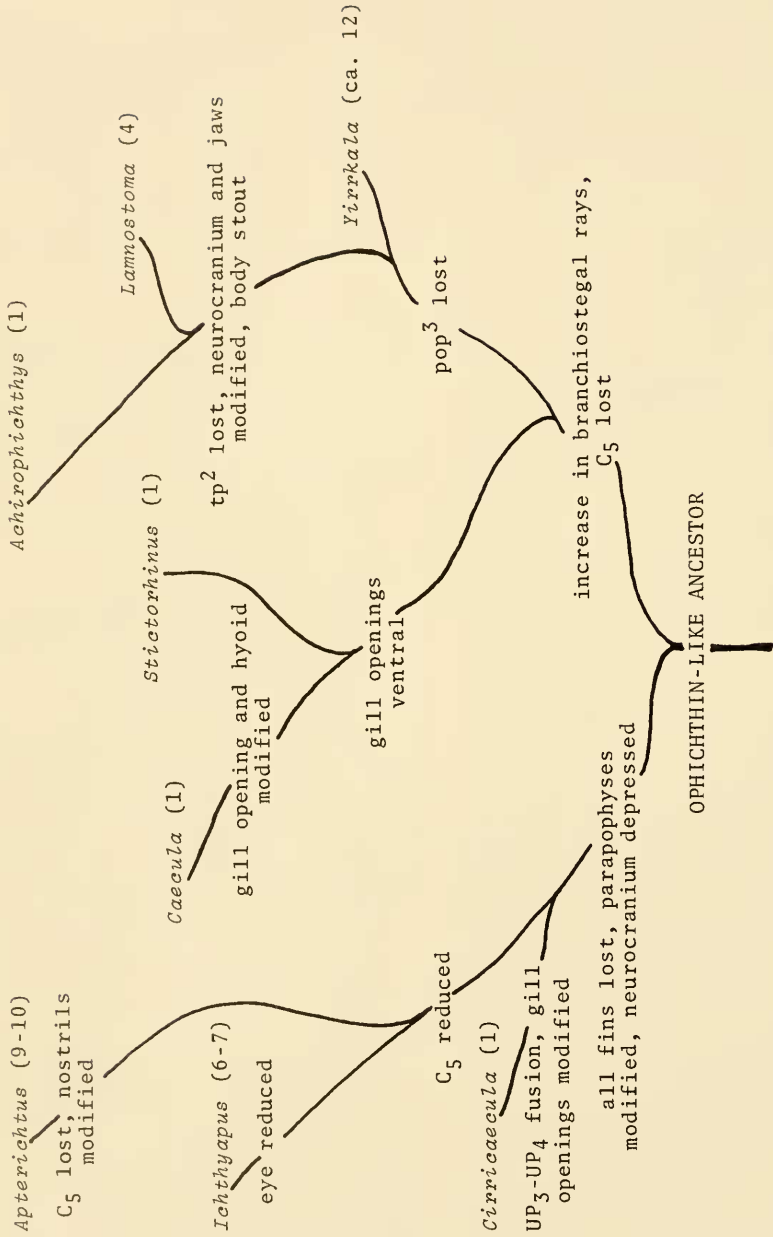


Figure 40. Proposed evolution of the Sphagebranchini.

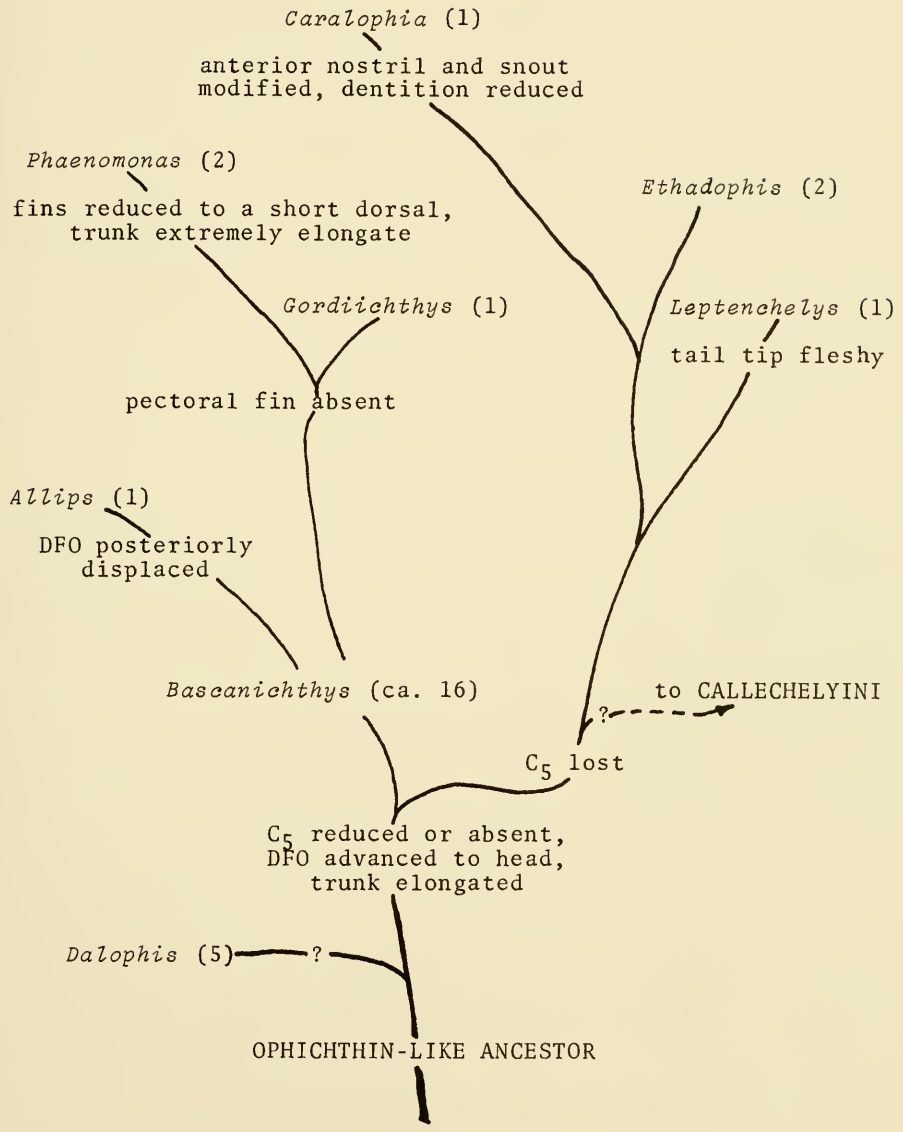


Figure 41. Proposed evolution of the Bascanichthyini.

the  $C_5$  and the posterior nostril is translocated to the outer lip.

The remaining genera are characterized by an increased number of branchiostegals and the loss of the  $C_5$ . They may be separated into two major lineages. *Caecula* and *Stictorhinus* are similar to the finless sphagebranchins in having ventral gill openings, pointed snouts, and moderately depressed neurocrania; these similarities, in part, may be adaptations to a similar mode of life. The derivation of *Yirrkala* and the closely-related *Achirophichthys* and *Lamnostoma* is somewhat uncertain. They have lost the  $pop^3$  and have low lateral to ventral gill openings. The neurocrania of these genera are considerably modified from the broad, depressed state of other sphagebranchins. The neurocranium of *Yirrkala* is rounded dorsally. That of *Lamnostoma* has become narrowed along the ethmoid, in probable correlation with its enlarged dentition and related to its feeding mode. Certain species of *Yirrkala* have retained the  $tp^2$ . The species of *Yirrkala* are generally elongate whereas those of *Achirophichthys* and *Lamnostoma* are cylindrical and stout.

*Bascanichthyini*. The *Bascanichthyini*, like the *Sphagebranchini*, appear to be derived from a moderately specialized ophichthin-like ancestor. Certain specializations in the form of hyoid modifications and fin reductions had already been achieved by their supposed ophichthin-like ancestor. As adults, the *bascanichthyins* have specialized toward a burrowing, vermiform existence, feeding on small prey and rarely leaving the substrate. As noted in the discussion of the axial skeleton (p. 45), the trunk elongation of species of *Phaenomonas*, *Allips*, certain *Bascanichthys* and presumably *Gordiichthys* is a specialization for this mode of life. Primitive conditions of certain characters within the *Bascanichthyini* include:

- (a) pectoral fin rudimentary;
- (b) eye small, but not minute;
- (c)  $C_5$  present, but reduced;
- (d) body and tail nearly subequal;
- (e) branchiostegal rays numerous;
- (f) DFO behind head;
- (g) snout grooved on underside;
- (h) gill openings low lateral in position.

The inclusion of *Dalophis* in the *Bascanichthyini* is uncertain. Although possessing *Ophichthus*-like body/tail proportions and an ossified  $C_5$ , it appears more similar to the *bascanichthyin* condition in its fin reductions and general ce-

phalic appearance. As a *bascanichthyin*, it is placed near the primary separation from the ancestral lineage (Fig. 41).

The remaining genera appear to be derived from the generalized condition of *Bascanichthys*. The rudimentary pectoral fin is retained only by *Allips*. *Allips* is similar to species of *Bascanichthys* in its trunk elongation and general physiognomy, but differs in its presumably secondarily-derived posterior DFO. *Phaenomonas* is further specialized through reduction from this lineage and has become nearly finless. *Gordiichthys*, not examined in this study, is provisionally referred to this lineage on the basis of characters included in its terse description. The remaining *bascanichthyins* are somewhat similar in their general morphologies, and have undergone several modifications and reductions from the *Bascanichthys* condition. The *Callechelyini* are herein assumed to be derived from a *bascanichthyin*-like ancestor, but have further specialized and radiated along a different complex of adaptive characters.

*Callechelyini*. The *Callechelyini* is the most distinct and compact of ophichthine tribes. The species are among the most specialized of ophichthids and are quite removed from the ancestral ophichthid stock. Their specializations and reductions impart a particular facies to the group that readily separates it from other ophichthids, particularly evidenced in the ventral, convergent gill openings, laterally compressed body, short tail, anterior dorsal fin origin, small eyes, and reduced pore systems. These outer similarities are borne out by the shortened neurocranium, stout hyoid, and the osteological reductions in the pectoral apparatus and gill arches which further characterize the group.

These conditions appear to have been derived from a *bascanichthyin*-like ancestor or from an ophichthin ancestor which gave rise to the *Bascanichthyini*. Available specimens or radiographs of 20 of the 22 species of the *Callechelyini* have allowed an in-depth study of this tribe. The meristic and morphological characters listed in Tables 8-9 were used to generate the computer-programmed taxonomic evaluations illustrated in Figures 43-44. The characteristics of computer programs WVGM and REGROUP are described in the taxonomic methods sections of this study.

Primitive conditions of certain key characters within the *Callechelyini* include:

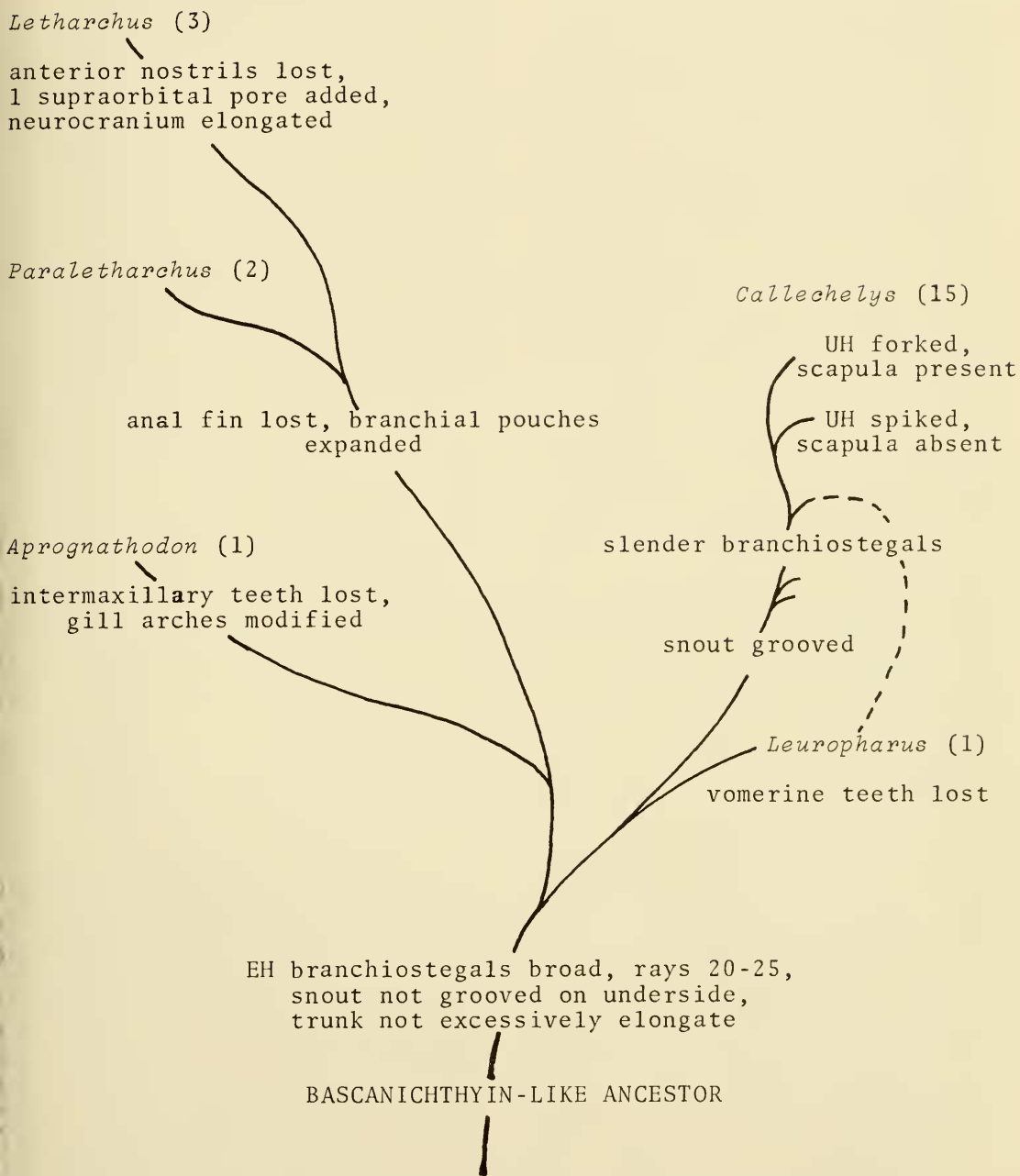


Figure 42. Proposed evolution of the Callechelyini.

- (a) teeth uniserial and present on the dentary, intermaxillary, maxilla, and vomer;
- (b) underside of snout not grooved;
- (c) gill openings low and bascanichthyin-like, not specialized as in *Letharchus* and *Paraletarchus*;
- (d) branchiostegal rays fewer than 25 pairs, those along the epiphyal broadened basally;
- (e) three supraorbital pores;
- (f) trunk not extremely elongate, tail 40 percent or more of total length;
- (g) urohyal ossified and spike-like, not forked posteriorly;
- (h) two longitudinal rod-like pectoral elements.

No living tribal member possesses all the primitive characters listed above. However *Aprognathodon platyventris* and certain species of *Callechelys*, except for minor specializations, closely approximate the above conditions.

The retention of several primitive characters suggests that *Aprognathodon platyventris* separated early from the basal stock (Fig. 42). It has become specialized through the loss of intermaxillary dentition and the incomplete re-ossification of the third hypobranchial. These conditions are probably adaptations to a specialized mode of feeding.

The next dichotomy in the tribal evolution involved two other New World genera, *Letharchus* and *Paraletarchus* (compare Figs. 42-44). They, like *Aprognathodon*, have retained the broad branchiostegals and ungrooved snouts, but are specialized in having broadly flared branchial pouches and in the loss of the anal fin. Species of *Paraletarchus* appear externally quite similar to species of *Callechelys*; species of *Letharchus* are quite distinctive in having lost the tubular anterior nostril condition, added a fourth supraorbital pore, and having more elongate and depressed neurocrania.

The remaining callechelyins include *Leuropharus lasiops* and the numerous species of *Callechelys*. *Leuropharus* is somewhat generalized in having few vertebrae, a moderate tail length, and an ungrooved snout, yet it differs from other callechelyins in lacking teeth on the vomer. Whether it separated before the species of *Callechelys* or from a *Callechelys*-like ancestor is questionable in that *L. lasiops* appears to have numerous, slender branchiostegals (observed from a radiograph of the type specimen). This condition, if observed correctly, is more advanced than that of certain species of *Callechelys* (*C. nebulosus*, *C. springeri*, and *C. holo-*

*chromus*), and would necessitate the parallel evolution of this condition if *Leuropharus* separated earlier than *Callechelys*.

The remaining genus, *Callechelys* with 15 recognized species, has apparently combined the generalized callechelyin condition with certain minor specializations into a very successful "body plan". Evolution within *Callechelys*, as discussed on page 63, has included two or three early separations from the ancestral stock, which were followed by two major subgeneric lines. *Callechelys nebulosus*, *C. springeri*, and perhaps *C. holo-chromus* have retained broadened branchiostegal rays, which is probably correlated to their moderate number. These two conditions are probably responsible for the separation of these species from other *Callechelys* species in programs WVGM and REGROUP (Figs. 43-44). These conditions should not preclude their inclusion within *Callechelys* and illustrates the weakness of a numerical taxonomic scheme based on too few characters. The remaining species are specialized in having more numerous and slender branchiostegal rays, and a longer trunk region and an increase in the number of trunk vertebrae. These species have evolved along two lineages, one containing species which have retained a simple urohyal and lost the posterior pectoral girdle element (the scapula?), and another with species in which the urohyal is split posteriorly into two slender divergent rays but with the second pectoral element retained. Neither of these specializations, when compared with those of other ophichthids, seems to merit generic separation.

#### Zoogeography and Comments on Ophichthid Speciation

In the absence of a suitable fossil record, it is virtually impossible to reconstruct with certainty the past distribution and center of origin of the Ophichthidae. Certain inferences relating to ancestral distributions however, can be made based on the present species distribution, assumed environmental tolerances of ophichthids in general, and the presumed geological history of tropical land and water masses.

Two major geological events have directly affected the distribution of tropical marine organisms. These were the Miocene (?) closure of the Tethyan Seaway through the convergence of the European and African continental plates (Phillips and Forsyth, 1972), isolating the Mediterranean and Atlantic from the Indo-Pacific, and the late



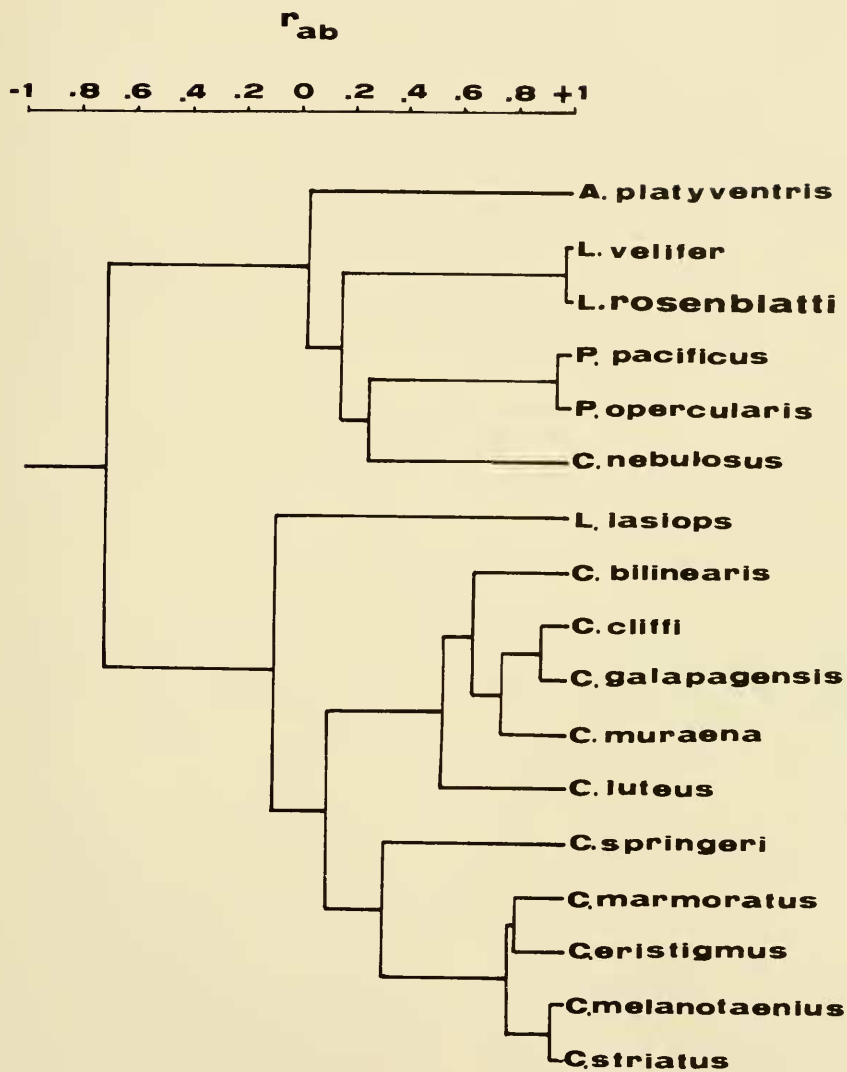


Figure 43. Phenogram of the relationships of the species of the Callechelyini, using program WVGM. The levels of correlation at which species join are represented by the scale  $r_{ab}$ .

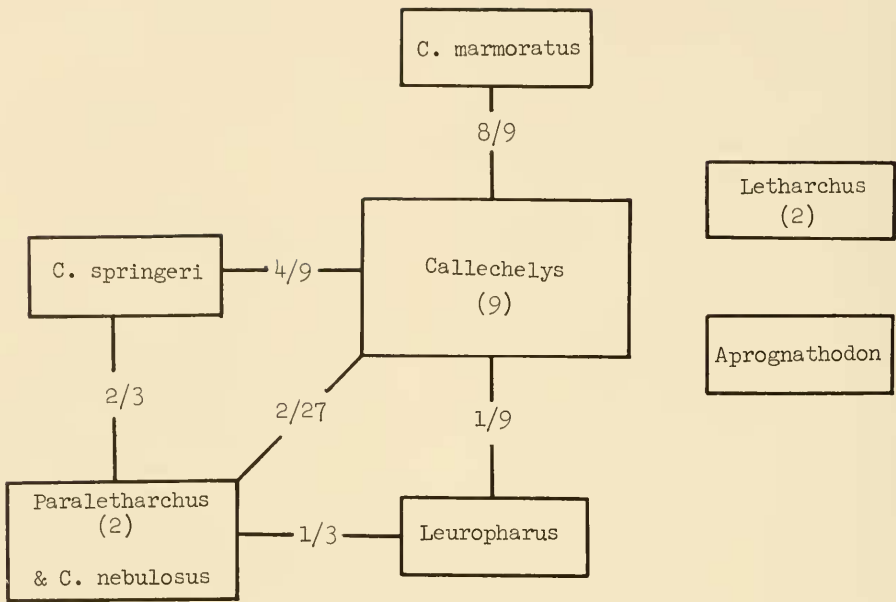


Figure 44. Interrelationships of species groups of the tribe Callechelyini, as defined by program REGROUP. Significance level set at 0.600. Fractions are the ratios of the number of observed between-group species connections to the maximum number of possible connections. Number of species represented per genus are within parentheses. Not included are *Callechelys bitaeniatus*, *C. holochromus*, *C. leucopterus*, and *Letharchus aliculatus*.

Pliocene to Pleistocene closure (Whitmore and Stewart, 1965) of the Middle American Seaway, separating the New World oceans (Rosenblatt, 1963). Assuming that the environmental tolerances of the Ophichthidae have always limited them to tropical, sub-tropical, or warm temperate waters, it may be stated that the Tethyan and Central American Seaway closures have delimited, in large part, the waters available to the distribution of living genera. (A single exception may be the distribution of *Ophisurus serpens* in the Mediterranean, and eastern and western African shores, probably resulting from a transgression of the Cape of Good Hope.) Applying these assumptions to the known distribution of ophichthid genera (Table 10), inferences concerning the evolution and generic interrelationships of the family may be drawn. For example, the seven circumtropical genera must have existed prior to the closure of the Tethyan Seaway, or have passed through the Central American Seaway

and transgressed both oceans. Recent information gained from investigations of plate tectonics and paleomagnetism suggests that the Atlantic Ocean during the Early Cretaceous was much narrower than at present (Phillips and Forsyth, 1972). On that basis, the distribution of an archaic species across the Tethyan Seaway and into the eastern Pacific would seem quite plausible.

An *Ophichthus*-like genus probably existed in the Upper Eocene, as evidenced by Storms' (1896) description of *Eomyrus dolloi* from the Wemmelian Formation of western Europe. The neurocranium, as illustrated, is much like that of a modern *Ophichthus*. Those genera restricted to both coasts of the New World (Table 10, Group III) must have existed prior to the Panamanian uplift, and now include several pairs of closely related species. *Echiophis* is also a member of this group but has presumably extended its distribution to the eastern Atlantic. The genus *Muraenichthys* is presently limited to the Red

Sea, Indian Ocean, western and central Pacific oceans, with a single south eastern Pacific species known only from the offshore Chilean islands of Juan Fernandez and San Felix. Its absence from the tropical Atlantic, as explained by McCosker (1970), perhaps suggests a post-Tethyan origin of the genus rather than the lack in the Atlantic of a suitable habitat. The single New World species is probably recently derived from the south-western Pacific by means of eastward transport across the South Pacific. The restriction of many genera to the Indo-Pacific and New World oceans (Table 10, Groups II, IV-V) probably represents radiations since the Tethyan and Central American Seaway closures, respectively. The origin of genera with species distributed across major water masses might be inferred from an analysis of the species involved. The genus *Phaenomonas*, for example, contains an eastern Pacific species (*P. pinnata*) which ranges from the Gulf of California to Colombia, and an Indo-Pacific species (*P. cooperae*) which ranges from Hawaii to east Africa. The extreme specialization of *P. cooperae*, in comparison to *P. pinnata*, might suggest that *Phaenomonas* arose in the eastern Pacific and radiated westward. Its presumed absence from the Atlantic Ocean would indicate that *Phaenomonas* either evolved from the bascanichthyin stock since the closure of the Central American Seaway, or that proper *Phaenomonas* habitat is presently unavailable in the Atlantic. Another explanation might assume that the present existence of the primitive *P. pinnata* in the eastern Pacific is the result of an eastward radiation from an Indo-Pacific origin, followed by further specialization of the ancestral stock through competition with the more complex ophichthid fauna of the Indo-Pacific. Caution however, must be applied in any of the above assumptions concerning the present distribution of ophichthid genera. Modern collecting methods have resulted in the discovery of numerous new species, many of which represented new genera, and it is highly likely that many extant ophichthid species remain uncollected.

An analysis of the distribution of species among ophichthid genera reveals several interesting biological phenomena. The classification proposed here is hopefully more than just a convenient cataloguing system, and assumes that the disproportionate number of species in various ophichthid genera, ranging from a single species in nearly half of the genera to more than

50 in *Ophichthus*, reflects something real in the natural system. Figure 45 illustrates the distribution of species among the genera of the Ophichthidae, Gobiessocidae, and the blenniid tribe Salariini. These examples were chosen because they represent recent monographic revisions, uncomplicated by the efforts of a multiplicity of authors; the gobiessocid data are from Briggs (1955) and subsequent species descriptions and the blenny data are based on Smith-Vaniz and Springer (1971). A pattern exists in the three groups illustrated, and if transformed to logs, the data would indicate an almost straight-line inverse relation between the log-number of species/genus and the log number of genera. C. B. Williams (1964) has discussed similar evidence from a number of terrestrial groups and suggested that such a log-normal mathematical pattern is a recurrent phenomenon in natural systems. He observed that the fit of these data to a calculated log series is moderately good at most levels, but higher than expected for monotypic genera.

The following hypotheses are proposed to explain the distribution of species among genera. One hypothesis might assume that such a distribution of species among genera reflects the evolution of a group with many recently-derived genera, and a decreasing number of genera which have existed for increasingly longer time spans. Those archaic genera have had the opportunity through geologic time and events to segregate and speciate, whereas the more recent taxa have lacked those opportunities. A more intriguing hypothesis however, suggested by Richard H. Rosenblatt (personal communication), might assume that a combination of characters exist in the ancestral lineage from which taxa radiate by means of specializations and reductions; certain resultant taxa would include a combination of characters which would allow further radiation (dependent upon certain biological factors and geological events) resulting in genera with numerous species, whereas other taxa have specialized in a manner which, in relation to the available environments, has a low probability of further radiation. The latter category contains the numerous monotypic genera of the Ophichthidae. These monotypic genera might represent evolutionary "forays" into rather unique environments or life styles and are apparently unsuccessful beyond their present limited area of distribution or as ancestral bases for further speciation. The former category, in which

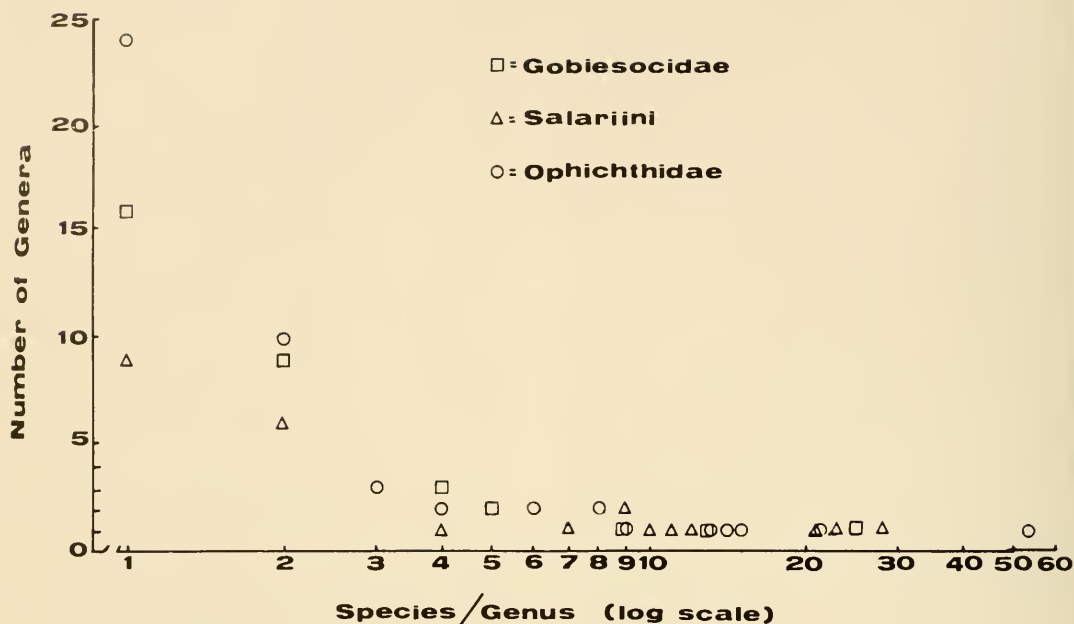


Figure 45. Distribution of species among the genera of the Ophichthidae, Gobiesocidae and Salariaiini.

few genera contain many species, contains such genera as *Myrichthys*, *Callechelys*, and *Ophichthus*, in which the combination of adaptive characters selected for have, with minor modifications, resulted in the numerous species which occupy similar habitats in all tropical oceans. Biological factors such as the leptocephalus larval stage and geological events such as seaway closures lend credence to the first mentioned

hypothesis and complicate the second. Yet the present distribution and few species of several presumably archaic ophichthid genera would tend to support the latter hypothesis.

Further investigations into the ecology and behavior of species of this intriguing and diverse eel family may offer further insight into the evolutionary processes which have shaped the Ophichthidae.

## LITERATURE CITED

- Ahl, J. N. 1789. *Dissertatio de Muraena et Ophichtho. Dissertationes Academicae Upsaliae habitae sub praesidio C. P. Thunberg*, 3(1): 1-12.
- Allis, E. P., Jr. 1903. The lateral sensory system in the Muraenidae. *Intern. Monats. Anat. Physiol.*, 20: 125-170.
- Asano, H. 1962. Studies of the Congrid eels of Japan. *Bull. Misaki Marine Biol. Inst.*, no. 1. 143 pp.
- Bamber, R. C. 1915. Reports on the marine biology of the Sudanese Red Sea, from collections made by Cyril Crossland . . . XII. The fishes. *Linn. J. Zool.*, 31: 477-485.
- Beebe, W. 1935. Deep-sea fishes of the Bermuda Oceanographic expeditions. No. 1 — Family Derichthyidae. *Zoologica*, N.Y., 20(1): 1-23.
- Bertin, L. 1935. *Oxystomus de Rafinesque est une forme bien distincte, parmi les larves leptocephaliennes. Comptes Rend. des séances de l'Acad. des Sci.*, 200: 1878.
- Bertin, L. and C. Arambourg. 1958. Super-ordre des Teleostéens. *Traité de Zoologie*, 13, fasc. 3: 2204-2500.
- Blache, J. 1968. Contribution à la connaissance des Poissons anguilliformes de la côte occidentale d'Afrique. Huitième note: la famille des *Echelidae*. *Bull. de l'I. F. A. N., sér. A*, 30(4): 1501-1539.
- Blache, J. 1971. Contribution à la connaissance des Poissons anguilliformes de la côte occidentale d'Afrique. Onzième note: les genres *Mystriophis* et *Echiopsis* (Fam. des *Ophichthidae*). *Bull. de l'I. F. A. N., sér. A*, 33(1): 202-226.
- Blache, J. and M. L. Bauchot. 1972. Contribution à la connaissance des Poissons anguilliformes de la côte occidentale d'Afrique. Troisième note: les genres *Verma*, *Apterichthus*, *Ichthyapus*, *Hemerorhinus*, *Caecula*, *Dalophis* avec la description de deux genres nouveaux (Fam. des *Ophichthidae*). *Bull. de l'I. F. A. N., sér. A*, 34(3): 692-773.
- Blache, J. and J. Cadenat. 1971. Contribution à la connaissance des Poissons anguilliformes de la côte occidentale d'Afrique. Dixième note: les genres *Myrichthys*, *Bascanichthys* et *Callechelys* (Fam. des *Ophichthidae*) *Bull. de l'I. F.A.N., sér. A*, 33(1): 158-201.
- Blache, J., J. Cadenat., and A. Stauch. 1970. Clés de détermination des Poissons de mer signalés dans l'atlantique oriental entre le 20<sup>e</sup> parallèle nord et le 15<sup>e</sup> parallèle sud. O. R. S. T. O. M., *Faune Tropicale*, 13. 479 pp.
- Bleeker,, P. 1853a. Dijdrage tot de kennis der Muraenoiden en Symbbranchoiden van den Indischen Archipel. *Verh. Batav. Genootsch.*, 25: 1-62.
- Bleeker, P. 1853b. Diagnostische beschrivnigen van nieuwe of wenig bekende wisschsoorten van Batavia. *Tintal I-VI, Nat. Tijdschr. Neder.-Indie*, 4: 451-516.
- Bleeker, P. 1863. Mémoire sur les poissons de la côte de Guinée. *Nat. Verh. Holl. Maatsch. Wet. Haarlem*, 2(18): 1-136.
- Bleeker, P. 1865. *Systema Muraenorum revisum. Neder. Tijdschr. Dierk.*, II, 1865: 113-122.
- Bloch, M. E. 1795. *Naturgeschichte der Ausländischen Fische. IX. (Not seen).*
- Böhlke, J. E. 1955. A new genus and species of ophichthid eels from the Bahamas. *Notul. Nat.*, no. 282: 1-7.
- Böhlke, J. E. 1956a. A synopsis of the eels of the family Xencongridae (including the Chlopsidae and Chilorhinidae). *Proc. Acad. Nat. Sci. Philadelphia*, 108: 61-95.
- Böhlke, J. E. 1956b. A small collection of new eels from western Puerto Rico. *Notul. Nat.*, no. 289: 1-13.
- Böhlke, J. E. 1960. A new ophichthid eel of the genus *Pseudomyrophis* from the Gulf of Mexico. *Notul. Nat.*, no. 329: 1-8.
- Böhlke, J. E. 1967. The descriptions of three new eels from the tropical West Atlantic. *Proc. Acad. Nat. Sci. Philadelphia*, 118(4): 91-108.
- Böhlke, J. E. 1968. A new species of the ophichthid eel genus *Verma* from the West Atlantic, with comments on related species. *Notul. Nat.*, no. 415: 1-12.
- Böhlke, J. E. and J. E. McCosker. 1975. The status of the ophichthid eel genera *Caecula* Vahl and *Sphagebranchus* Bloch, and the description of a new genus and species from fresh waters in Brazil. *Proc. Acad. Nat. Sci. Philadelphia*, 127(1): 1-11.
- Böhlke, J. E. and C. R. Robins. 1959. The characters and synonymy of the Western Atlantic snake eel, *Ophichthus ophis* Linnaeus. *Notul. Nat.*, no. 320: 1-9.
- Briggs, J. C. 1955. A monograph of the clingfishes (order Xenopterygii). *Stanford Ichthyol. Bull.*, 6: 1-224.
- Burton, P. R. 1956. A comparative osteological study of the skulls of the moray eels, *Gymnothorax funebris* Ranzani and *Gymnothorax moringa* (Cuvier). *J. Florida Acad. Sci.*, 19(1):

- 35-44.
- Castle, P. H. J. 1963. The systematics, development and distribution of two eels of the genus *Gnathophis* (Congridae) in Australian waters. Zool. publ. Victoria Univ. New Zeal., no. 34: 15-47.
- Castle, P. H. J. 1965. Ophichthid leptocephali in Australian waters. Trans. roy. Soc. N. Z., 7(6): 97-123.
- Castle, P. H. J. 1967. Two remarkable eel-larvae from off Southern Africa. Spec. Publ. Inst. Ichthyol. Rhodes Univ., (1): 1-12.
- Castle, P. H. J. 1969. An index and bibliography of eel larvae. Spec. Publ. Inst. Ichthyol. Rhodes Univ., (7): 1-121.
- Castle, P. H. J. 1972. The eel genus *Benthenchelys* (fam. Ophichthidae) in the Indo-Pacific. Dana-Rep., no. 82. 32 pp.
- Chabanaud, P. 1936. Le neurocrane osseux des Téléostéens dyssymétriques. Ann. Inst. Oceanogr., n. s., 16(3): 223-297.
- Chan, W. L. 1967. A new species of congrid eel from the South China Sea. J. nat. Hist., 1: 97-112.
- Cohen, D. M. and D. Dean. 1970. Sexual maturity and migratory behaviour of the tropical eel, *Ahlia egmontis*. Nature, 227(5254): 189-190.
- Cope, E. D. 1871. Contribution to the ichthyology of the Lesser Antilles. Trans. Amer. Phil. Soc., 14(2): 445-583.
- Cuvier, G. L. C. F. D. 1817. Le règne animal distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Les reptiles, les poissons, les mollusques et les annélides. Deterville, Paris, 2: 1-532.
- de Barneville, B. 1847. Note sur un nouveau genre d'anguilliformes. Rev. Zool., 1847: 219-220.
- Deraniyagala, P. E. P. 1929. Some anguilliform fishes of Ceylon. Spolia Zeylandica, 15(1): 1-29.
- Duméril, A. M. C. 1806. Zoologie analytique, ou methode naturelle de classification des animaux. Paris. 344 pp.
- Duméril, A. M. C. 1856. Ichthyologie analitique ou classification des poissons, suivant la methode naturelle, à l'aide de tableaux synoptiques. Mém. Acad. Sci. Paris, 27, pt. 1. 511 pp.
- Ebeling, A. W. and W. H. Weed. 1963. Melamphaidae III. Systematics and distribution of the species in the bathypelagic fish genus *Scopelogadus* Vaillant. Dana-Rep., no. 60. 58 pp.
- Eldred, B. 1966. The early development of the spotted worm eel. *Myrophis punctatus* Lütken (Ophichthidae). Florida Bd. Conserv. Mar. Lab., leaf. ser., 4(1): 1-13.
- Fager, E. W. 1957. Determination and analysis of recurrent groups. Ecology, 38(4): 586-595.
- Fager, E. W. 1969. Recurrent group analysis in the classification of flexibacteria. J. gen. Microbiol., 58: 179-187.
- Fager, E. W. and A. R. Longhurst. 1968. Recurrent group analysis of species assemblages of demersal fish in the Gulf of Guinea. J. Fish. Res. Bd. Canada, 25 (7): 1405-1421.
- Fager, E. W. and J. A. McGowan. 1963. Zooplankton species groups in the North Pacific. Science, 140(3566): 453-460.
- Fischer von Waldheim, G. 1813. Zoognosia, Tabulus Synopticus Illustrata. Ed. III, vol. 1. (Not seen).
- Fowler, H. W. 1918. New and little-known fishes from the Philippine Islands. Proc. Acad. Nat. Sci. Philadelphia, 70: 2-71.
- Fowler, H. W. 1925. New taxonomic names of West African marine fishes. Amer. Mus. Novitates, 162: 1-5.
- Fowler, H. W. 1934. Descriptions of new fishes obtained 1907 to 1910, chiefly in the Philippine Islands and adjacent seas. Proc. Acad. Nat. Sci. Philadelphia, 85: 233-267.
- Fowler, H. W. 1936. The marine fishes of West Africa. Part I. Bull. Amer. Mus. Nat. Hist., 70: 1-605.
- Fowler, H. W. 1938. The fishes of the George Vanderbilt South Pacific Expedition, 1937. Monogr. Acad. Nat. Sci. Phila. no. 2. 349 pp.
- Fowler, H. W. 1944. Results of the Fifth George Vanderbilt Expedition (1941). Monogr. Acad. Nat. Sci. Phila. no. 6: 57-529.
- Frizzell, D. L. and C. K. Lamber. 1962. Distinctive "Congrid type" fish otoliths from the Lower Tertiary of the Gulf Coast (Pisces: Anguilliformes). Proc. Cal. Acad. Sci., 4th ser., 32(5): 87-101.
- Frost, G. A. 1926. A comparative study of the otoliths of the Neopterygian fishes (continued). III. Order Apodes. Ann. Mag. Nat. Hist., ser. 8, 10: 99-104.
- Ganguly, D. N. and A. C. Nag. 1964. On the functional morphology of the pectoral girde and the acranial myomeric musculature of a benthozoic teleostean fish *Ophichthys boro* (Ham. Buch.). Anat. Anz., 115: 405-417.
- Ginsburg, I. 1951. The eels of the northern Gulf Coast of the United States and some related species, Texas J. Sci., 3(3): 431-485.
- Girard, C. F. 1859. Ichthyological notices. Proc.

- Acad. Nat. Sci. Philadelphia, 1859(1860): 56-58.
- Gistel, J. 1848. Naturgeschichte des Thierreichs für höhere Schiler. (Not seen.)
- Glover, T. A. 1973. Fishes of southern and western Japan, vol. 1 (groups 1-7). Nagasaki Univ. 429 pp. (In Japanese.)
- Goode, G. B. and T. H. Bean. 1882. Descriptions of twenty-five new species from the Southern United States, and three new genera, *Letharchus*, *loglossus*, and *Chriodorus*. Proc. U. S. Nat. Mus., 1882, 5: 412-437.
- Goodrich, E. S. 1930. Studies on the structure and development of vertebrates. 8 London. 837 pp.
- Gosline, W. A. 1950. The osteology and relationships of the echelid eel, *Kaupichthys diodontus*. Pacific Sci., 4(4): 309-314.
- Gosline, W. A. 1951a. The osteology and classification of the ophichthid eels of the Hawaiian Islands. Pacific Sci., 5(4): 298-320.
- Gosline, W. A. 1951b. *Chilorhinus brocki*, a new echelid eel from Hawaii, with notes on the classification of the order Anguillida. Copeia, 1951(3): 195-202.
- Gosline, W. A. 1952. Notes on the systematic status of four eel families. J. Wash. Acad. Sci., 42(4): 130-135.
- Gosline, W. A. 1959. Mode of life, functional morphology, and the classification of modern teleostean fishes. Syst. Zool., 8(3): 160-164.
- Gosline, W. A. 1971. Functional morphology and classification of teleostean fishes. Honolulu, Univ. Hawaii Press. 208 pp.
- Grassi, G. B. 1913. Metamorfosi dei murenoidi. Ricerche sistematiche ed ecologiche. Jena, Fischer. 211 pp. (Not seen.)
- Greenwood, P. H., D. E. Rosen, S. H. Weitzman, and G. S. Myers. 1966. Phyletic studies of teleostean fishes, with a provisional classification of living forms. Bull. Amer. Mus. Nat. Hist., 131: 345-455.
- Günther, A. 1870. Catalogue of the fishes in the British Museum. Vol. VIII, Catalogue of the Physostomi. London, Taylor and Francis. 549 pp.
- Günther, A. 1910. Andrew Garrett's Fische des Südsee, . . . Heft IX. J. Mus. Godeffroy, Hamburg, Heft 17: 389-515.
- Harry, R. R. 1948. New records for the fish *Myrichthys tigrinus*, a snake eel of the eastern tropical Pacific, with a relocation of the type locality. Copeia, 1948(2): 145-146.
- Hector, J. 1870. On a species of *Ophisurus* found on the coast of New Zealand. Trans. Proc. N. Z. Inst., 1869(1870), 2: 34-40.
- Herre, A. W. C. T. 1924. Some rare Philippine eels. Philipp. J. Sci., 24(1): 107-111.
- Hiatt, R. W. and D. W. Strasburg. 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecol. Monographs, 30: 65-127.
- Hopkirk, J. D. 1965. Records of yellow and spotted snake-eels (genus *Ophichthus*) from San Francisco Bay, California. Cal. Fish and Game, 51(3): 183-186.
- Hubbs, C. L. 1932. The use of the generic name *Ophis* for an eel, a snake and a mollusc. Copeia, 1932(1): 26-27.
- Jordan, D. S. 1919a. New genera of fishes. Proc. Acad. Nat. Sci. Philadelphia, 1918(1919), 70: 341-344.
- Jordan, D. S. 1919b. The genera of fishes, part II, from Agassiz to Bleeker, 1833-1858, twenty-six years, with the accepted type of each. A contribution to the stability of scientific nomenclature. Leland Stanford Jr. Univ. Pub., Univ. ser.: 163-284.
- Jordan, D. S. 1932. The "first species" and the "first reviser". Science, 25(638): 467-469.
- Jordan, D. S. and B. M. Davis. 1891. A preliminary review of the apodal fishes or eels inhabiting the waters of America and Europe. Rep. U.S. Comm. of Fish and Fisheries for 1888, part 16: 581-677.
- Jordan, D. S. and B. W. Evermann. 1896. The fishes of North and Middle America: A descriptive catalogue . . . Panama. Part I. Bull. no. 47, U. S. Nat. Mus. 1240 pp.
- Jordan, D. S. and B. W. Evermann. 1905. The aquatic resources of the Hawaiian Islands. Part I. The shore fishes. U. S. Bur. Fisheries, Bull. 1903, 23(1): 1-574.
- Jordan, D. S. and C. H. Gilbert. 1882. Descriptions of thirty-three new species of fishes from Mazatlan, Mexico. Proc. U. S. Nat. Mus., 4: 338-365.
- Jordan, D. S. and C. H. Gilbert. 1883. On the nomenclature of the genus *Ophichthys*. Proc. U. S. Nat. Mus., 5: 648-651.
- Jordan, D. S. and J. O. Snyder. 1901. A review of the apodal fishes or eels of Japan, with descriptions of 19 new species. Proc. U. S. Nat. Mus., 23(1239): 837-890.
- Kanazawa, R. H. 1963. Two new species of ophichthid eels from the western Atlantic. Proc. Biol. Soc. Wash., 76: 281-288.
- Kaup, J. 1856a. Übersicht der Aale. Arch. Na-

- turges., 22(1): 41-77.
- Kaup, J. 1856b. Catalogue of apodal fish in the collection of the British Museum. London. 160 pp.
- Kaup, J. 1860. Neue aalähnliche Fische des Hamburger Museums. Abh. Natur. Verein Hamburg, 1859(1860), 4, Abth. 2. 35 pp.
- Knox, F. J. 1870. Anatomical observations on *Ophisurus novaehelandiae*. Trans. Proc. N. Z. Inst., 1869(1870), 2: 34-40.
- Kotthaus, A. 1968. Fische des Indischen ozeans, ergebnisse der ichthyologen, untersuchungen . . . III Ostariophysi und Apodes. "Meteor" Forschungsergeb Ser. D (Biol.), (3): 14-56.
- Lacépède, (Comte) B. G. E. (here called Citoyen La Cépède). 1800. Histoire Naturelle des Poissons, Vol. II. Paris. 413 pp.
- La Monte, F. 1961. *Achirophichthys kampeni* from Papua. Copeia, 1961(1): 115-116.
- Liddell, H. G. and R. Scott. 1901. A Greek-English lexicon. 8th edit. Oxford, Clarendon Press. 1776 pp.
- Linnaeus, C. 1758. Systema Naturae. Regnum Animalie. Guilielmi Engeleman, Lipsiae. 824 pp.
- Longley, W. H. and S. F. Hildebrand. 1941. Systematic catalogue of the fishes of Tortugas, Florida. Papers from Tortugas Lab., vol. 34, Carnegie Inst. Wash. Publ. 535. 331 pp.
- Lozano Rey, D. L. 1947. Peces Ganoideos y Fiso-stomos. Mem. Real Acad. Cien. Exactas, Fisicas y Nat. de Madrid. Ser. de Cien. Nat., 11. 839 pp.
- Lütken, C. F. 1851. Nogle bemaerkinger om naeseborenes . . . aalefamilien. Vidensk. Meddel. Naturhist. Foren. Kjobenjavn. 21 pp. (Not seen).
- Mattioli, P. A. 1568. Les commentaires de M. P. A. Matthiole . . . sur les six livres de P. Discoride . . . de la matière médicinale . . . mis en Francais sur la dernière édition Latine de l'auteur par M. J. des Moulins. Lyon. 819 pp. (Not seen).
- McAllister, D. E. 1968. Evolution of branchiostegals and classification of teleostome fishes. Bull. Nat. Mus. Canada, 221: 1-239.
- McClelland, J. 1844. Apodal fishes of Bengal. J. Nat. Hist. Calcutta, 5: 150-226.
- McCosker, J. E. 1970. A review of the eel genera *Leptenchelys* and *Muraenichthys*, with the description of a new genus, *Schismorhynchus*, and a new species, *Muraenichthys chilensis*. Pacific Sci., 24(4): 506-516.
- McCosker, J. E. 1972. Two new genera and two new species of western Pacific snake-eels (Apodes: Ophichthidae). Proc. Cal. Acad. Sci., 4th ser., 39(10): 111-120.
- McCosker, J. E. 1973. The osteology, classification, and relationships of the eel family Ophichthidae (Pisces, Anguilliformes). PhD diss., Univ. Calif. San Diego. 289 pp.
- McCosker, J. E. 1974. A revision of the ophichthid eel genus *Letharchus*. Copeia, 1974(3): 619-629.
- McCosker, J. E. In Press. The eel genus *Phaenomonas* (Pisces: Ophichthidae). Pacific Sci.
- McCosker, J. E. and R. H. Rosenblatt. 1972. Eastern Pacific snake-eels of the genus *Callechelys* (Apodes: Ophichthidae). Trans. San Diego Soc. Nat. Hist., 17(2): 15-24.
- Miller, R.V. and J. V. Landingham. 1969. Additional procedures for effective enzyme clearing and staining of fishes. Copeia, 1969(4): 829-830.
- Mohamed, K. H. 1958. On the occurrence of the eel *Neeenchelys buitendijki* Weber and de Beaufort in Indian waters. J. Bombay Nat. Hist. Soc., 55: 511-517.
- Myers, G. S. and M. H. Storey. 1939. *Hesperomyrus fryi*, a new genus and species of echelid eels from California. Stanford Ichthyol. Bull., 1(4): 156-159.
- Myers, G. S. and C. B. Wade. 1941. Four new genera and ten new species of eels from the Pacific coast of tropical America. Allan Hancock Pac. Exped., 9(4): 65-111.
- Nelson, G. J. 1966a. Gill arches of teleostean fishes of the order Anguilliformes. Pacific Sci., 20(4): 391-408.
- Nelson, G. J. 1966b. Osteology and relationships of the eel, *Neeenchelys buitendijki*. Copeia, 1966(2): 321-324.
- Nelson, G. J. 1967. Notes on the systematic status of the eels *Neeenchelys* and *Myroconger*. Pacific Sci., 21(4): 562-563.
- Nelson, G. J. 1969. Gill arches and the phylogeny of fishes with notes on the classification of vertebrates. Bull. Amer. Mus. Nat. Hist., 141: 479-522.
- Nelson, G. J. 1972. Cephalic sensory canals, pitlines, and the classification of esocid fishes, with notes on galaxiids and other teleosts. Amer. Mus. Novitates, no. 2492. 49 pp.
- Nichols, J. T. 1955. Results of the Archbold Expeditions. No. 71. Two new freshwater fishes from New Guinea. Amer. Mus. Novitates, no. 1735. 6 pp.
- Norman, J. R. 1922. A new eel from Tobago. Ann.



- Mag. Nat. Hist., ser. 9, 10: 296-297.
- Norman, J. R. 1926. The development of the chondrocranium of the eel (*Anguilla vulgaris*), with observations on the comparative morphology and development of the chondrocranium in bony fishes. Phil. Trans. R. Soc., ser. B, 214: 369-464.
- Nybelin, O. 1963. Zur morphologie und Terminologie des Schwanzskelettes der Actinopterygien. Arkiv für Zoologi, ser. 2, 15(35): 485-516.
- Ogilby, J. D. 1897. Some new genera and species of fishes. Proc. Linn. Soc. New South Wales, part 2: 245-251.
- Parr, A. E. 1930. Jugostegalia, an accessory skeleton in the gill cover of the eels of the genus *Myrophis*. Copeia, 1930(3): 71-73.
- Parra, D. A. 1877. Descripción de diferentes piezas de historia natural, las mas del reino marítimo, representadas en setenta y cinco laminas. Havana. (Not seen).
- Peden, A. E. 1972. Redescription and distribution of the rare deep sea eel *Xenomystax atrarius* in the eastern Pacific Ocean. J. Fish. Res. Bd. Canada, 29: 1-12.
- Pellegrin, J. 1912. Sur une collection de poissons des Nouvelles-Hebrides du Dr. Cailliot. Bull. Mus. Hist. Nat., Paris, 18(4): 205-207.
- Phillipps, W. J. 1926. New or rare fishes of New Zealand. Trans. Proc. N. Z. Inst., 56: 529-537.
- Phillips, J. D. and D. Forsyth. 1972. Plate tectonics, paleomagnetism, and the opening of the Atlantic. Bull. Geol. Soc. Amer., 83(6): 1579-1600.
- Poey y Aloy, F. 1867. Monografía de las Morenas Cubanas. Repertorio Físico-Natural de la Isla de Cuba, II: 245-268.
- Poey y Aloy, F. 1880. Revisio piscium cubensum. Anal. Soc. Hispanola Hist. Nat., Madrid, 9: 243-261. (Not seen).
- Popta, C. M. L. 1904. Les arcs branchiaux de quelques Muraenidae. Ann. Sci. Nat., 19: 367-390.
- Rafinesque-Schmaltz, C. S. 1810a. Caratteri di Alcuni Nuovi Generi e Nuove Species di Animal e Piante della Sicilia. Pub. April 1, 1810.
- Rafinesque-Schmaltz, C. S. 1810b. Indice d'Ittiologia Siciliana. Pub. May, 1810.
- Rafinesque-Schmaltz, C. S. 1815. Analyse de la Nature, ou Tableau dell'Univers et des Corps Organises "La Nature est mon Guide et Linnæus mon maitre." Palermo. 224 pp.
- Randall, J. E. and J. E. McCosker. 1975. The eels of Easter Island with a description of a new moray. Los Angeles County Mus., Contrib. in Sci., no. 264. 32 pp.
- Randall, J. E. and C. R. Robins. 1966. *Acanthenchelys spinicauda* Norman, a valid West Indian species of the snake-eel genus *Ophichthus*. Copeia, 1966(3): 610-611.
- Regan, C. T. 1912. The osteology and classification of the teleostean fishes of the order Apodes. Ann. Mag. Nat. Hist., 8th ser., (10): 377-387.
- Richardson, J. 1844a. The zoology of the voyage of H. M. S. Sulphur under the command of Captain Sir Edward Belcher . . . during the years 1836-42, no. 5, Ichthyology. Part 1: 51-70.
- Richardson, J. 1844b. Ichthyology of the voyage of H. M. S. Erebus and Terror, under the Command of Captain Sir James Clark Ross, R. N., F. R. S. Edward, Newman, London. 139 pp.
- Robins, C. H. 1971. The comparative morphology of the synphobranchid eels of the straits of Florida. Proc. Acad. Nat. Sci. Philadelphia, 123(7): 153-204.
- Robins, C. H. and C. R. Robins. 1967. The xencongrid eel *Chlopsis bicolor* in the western North Atlantic. Bull. Mar. Sci., 17(1): 232-248.
- Robins, C. H. and C. R. Robins. 1970. The eel family Dysommidae (including the Dysommidae and Nettodaridae), including a new genus and species. Proc. Acad. Nat. Sci. Philadelphia, 122(6): 293-335.
- Robins, C. H. and C. R. Robins. 1971. Osteology and relationships of the eel family Macrocephenchelyidae. Proc. Acad. Nat. Sci. Philadelphia, 123(6): 127-150.
- Rosenblatt, R. H. 1963. Some aspects of speciation in marine shore fishes. Systematics Assoc. Publ. No. 5: 171-180.
- Rosenblatt, R. H. 1967. The osteology of the congrid eel *Gorgasia punctata* and the relationships of the Heterocongrinae. Pacific Sci., 21(1): 91-97.
- Rosenblatt, R. H. and J. E. McCosker. 1970. A key to the genera of the ophichthid eels, with descriptions of two new genera and three new species from the eastern Pacific. Pacific Sci., 24(4): 494-505.
- Rosenblatt, R. H., J. E. McCosker and I. Rubinoff. 1972. Indo-west Pacific fishes from the Gulf of Chiriqui, Panama. Los Angeles County Mus., Contrib. in Sci., no. 234. 18 pp.
- Rosenblatt, R. H. and I. Rubinoff. 1972. *Pythonichthys asodes*, a new heterenchelyid eel from the Gulf of Panama. Bull. Mar. Sci. 22(2): 355-

- 364.
- Rüppell, E. 1826-1828. Atlas zu der Reise in Nördlichen Afrika: Fische des Rothen Meeres. 4 vols. (Not seen).
- Schultz, L. P. 1942. The first record of the ophichthyid eel *Scytalichthys miurus* (Jordan and Gilbert) from the Galapagos Islands, with notes on *Mystriophis interinctus* (Richardson). J. Wash. Acad. Sci., 32(3): 83.
- Schultz, L. P. 1943. Fishes of the Phoenix and Samoan Islands. Bull. U. S. Nat. Mus., 180. 316 pp.
- Schultz, L. P. and O. Barton. 1960. A redescription of *Letharchus pacificus*, a snake eel from the Eastern Pacific Ocean. Copeia, 1960(4): 351-353.
- Schultz, L. P. and collaborators. 1953. Fishes of the Marshall and Marianas Islands. Families from Asymmetrionidae through Siganidae. Bull. U. S. Nat. Mus., 202, 1. 685 pp.
- Schultz, L. P. and L. P. Woods. 1949. Keys to the genera of echelid eels and the species of *Muraenichthys* of the Pacific, with two new species. J. Wash. Acad. Sci., 39(5): 169-174.
- Schwartz, E. and A. D. Hasler. 1966. Superficial lateral line sense organs of the mudminnow (*Umbra limi*). Zeitschr. Vergleich. Physiol., 53(3): 317-327.
- Smith, A. 1847. Illustrations from the Zoology of South Africa; consisting chiefly of figures and descriptions of objects of natural history collected during an expedition into the interior of South Africa in 1834-1836. (Not seen).
- Smith, D. G. 1971. Osteology and relationships of the congrid eels of the western north Atlantic (Pisces, Anguilliformes). PhD diss., Univ. Miami. 163 pp.
- Smith, D. G. and P. H. J. Castle. 1972. The eel genus *Neoconger* Girard: systematics, osteology, and life history. Bull. Mar. Sci., 22(1): 196-249.
- Smith, J. L. B. 1957. The fishes of Aldabra. Part IX (with a new eel from East Africa). Ann. Mag. Nat. Hist., ser. 12, 10: 833-842.
- Smith, J. L. B. 1962. Sand-dwelling eels of the western Indian ocean and the Red Sea. Rhodes Univ. Ichthyol. Bull. 24: 447-466.
- Smith, J. L. B. 1964. The discovery in Mozambique of the little known eel *Ophichthys tenuis* Gunther, 1870, a redescription of the type of *Caecula pterygera* Vahl, 1794, notes on other species and on generic relationships. Ann. Mag. Nat. Hist., ser. 13, 7: 711-723.
- Smith-Vaniz, W. F. and V. G. Springer. 1971. Synopsis of the tribe Salariini, with descriptions of five new genera and three new species. Smithsonian. Contrib. to Zool., 73: 1-72.
- Sokal, R. R. and C. D. Michener. 1958. A taxonomic method for evaluating systematic relationships. Univ. Kansas Sci. Bull., 38: 1409-1438.
- Springer, S. and M. J. Allen. 1932. A peculiar snake-eel from the Gulf of Mexico. Copeia, 1932(2): 105.
- Springer, V. G. 1968. Osteology and classification of the fishes of the family Blenniidae. Bull. U. S. Nat. Mus., 284. 85 pp.
- Storey, M. H. 1939. Contributions toward a revision of the ophichthyid eels I. The genera *Callechelys* and *Bascanichthys*, with descriptions of new species and notes on *Myrichthys*. Stanford Ichthyol. Bull., 1(3): 61-84.
- Storms, R. 1896. Première note sur les poissons wemmeliens (Eocène supérieur) de la Belgique. Bull. Soc. Belge de Géol., de Paleont. et d'Hydrog., 10: 198-240.
- Swainson, W. 1838. The natural history of fishes, amphibians, and reptiles, or monocardian animals. Longmans, London, vol. 1. 368 pp.
- Taylor, W. R. 1967. An enzyme method of clearing and staining small vertebrates. Proc. U. S. Nat. Mus., 122(3596): 1-17.
- Tilak, R. and S. K. Kanji. 1967. Studies on the morphology of the pectoral girdle of *Pisodonophis boro* (Ham.) in relation to its habit. Anat. Anz., 120: 404-408.
- Tortonese, E. 1959. Contributo allo studio degli Ophichthidae del Mediterraneo (pisces anguilliformes). Annal. Mus. Civ. Stor. Nat. Genova, 71: 233-247.
- Tortonese, E. 1964. Contributo allo studio sistematico e biogeografico del pesci della Nuova Guinea. Annal. Mus. Civ. Stor. Nat. Genova, 75: 13-98.
- Trewavas, E. 1932. A contribution to the classification of the fishes of the order Apodes, based on the osteology of some rare eels. Proc. Zool. Soc. London, part 3: 639-659.
- Turton, W. 1807. The British fauna, containing a compendium of the zoology of the British Islands; arranged according to the Linnaean system. Swansea, London. 230 pp. (Not seen).
- Vahl, M. 1794. Beskrivelse af en nye fiskeslaegt. Skrivt. Naturh. Selsk. Kiobenhavn 3(2): 149-156. (Not seen).

- Wade, C. B. 1946. Two new genera and five new species of apodal fishes from the eastern Pacific. *Allan Hancock Pac. Exped.*, 9(7): 181-213.
- Weber, M. and L. F. de Beaufort. 1916. The fishes of the Indo-Australian Archipelago. III. Ostariophysii: II Cyprinoidea, Apodes, Synbranchi. Leiden. 455 pp.
- Whitley, G. P. 1930. Five new generic names for Australian fishes. *Austr. Zool.*, 6(3): 250-251.
- Whitley, G. P. 1934. Studies in Ichthyology. No. 8. *Rec. Australian Mus.*, 19(2): 153-163.
- Whitley, G. P. 1940. Illustrations of some Australian fishes. *Austr. Zool.*, 9(4): 397-428.
- Whitley, G. P. 1950. New fish names. *Proc. R. Zool. Soc. New South Wales, 1948-1949*: 44.
- Whitley, G. P. 1951. Studies in ichthyology. No. 15. *Rec. Australian Mus.*, 22(4): 389-408.
- Whitley, G. P. 1968. A check-list of the fishes recorded from the New Zealand region. *Austr. Zool.*, 15(1): 1-102.
- Whitmore, F. J., Jr. and R. H. Stewart. 1965. Miocene mammals and Central American seaways. *Science*, 148(3667): 180-185.
- Williams, C. B. 1964. Patterns in the balance of nature and related problems in quantitative ecology. Academic Press, London. 324 pp.
- Wormuth, J. H. 1971. The biogeography, systematics and interspecific relationships of the oegopsid squid family Ommastrephidae in the Pacific Ocean. PhD diss., Univ. Calif., San Diego. 189 pp.
- Ypiranga Pinto, S. 1970. Observacoes ictiologicas. VI — *Antobrantia*, novo genero de ofictideo do Brasil (Actinopterygii, Anguilliformes, Ophichthyidae). *Atas da Sociedade de Biologia do Rio de Janeiro*, 14 (1-2): 13-15.

Table 1. Dentition of the Genera of Ophichthidae

Abbreviations are: +, present; -, absent. Shape: C, conical; F, fang-like; M, molariform; V, villiform. Rows in jaws and vomer: B, biserial; M, multi-serial; U, uniserial. I-V signifies intermaxillary-vomerine.

	Shape	Rows in Jaws	Vomer	I-V Gap
<b>Benthenchelyini</b>				
<i>Benthenchelys</i>	C	U	U	+
<b>Myrophini</b>				
<i>Ahlia</i>	C	U	-	-
<i>Muraenichthys</i>	C,M	U,B,M	U,B	-
<i>Myrophis</i>	C	U,B	U,B	-
<i>Neenchelys</i>	C	U	B	-
<i>Pseudomyrophis</i>	C	U	U	-
<i>Schismorhynchus</i>	C	U	U	-
<i>Schultzidia</i>	V	U	-	
<b>Callechelyini</b>				
<i>Aprognathodon</i> <sup>1</sup>	C	U	U	-
<i>Callechelys</i>	C	U	U,B	+
<i>Letharchus</i>	C	U	U	+
<i>Leuropharus</i>	C	U	-	
<i>Paraletharchus</i>	C	U	U	+
<b>Sphagebranchini</b>				
<i>Achinopichthys</i>	C,F	B	U	?
<i>Apterichtus</i>	C	U	U	+
<i>Caecula</i>	C	U	U	+
<i>Cirriacaecula</i>	C	U	U	+
<i>Hemerorhinus</i>	?	?	?	?
<i>Ichthyapus</i>	C	U	U	+
<i>Lamostoma</i>	C,F	U,B	U	+
<i>Stictorhinus</i>	C	U	U	+
<i>Yirrkala</i>	C	U	U	+
<b>Bascanichthyini</b>				
<i>Allips</i>	C	U	U	+
<i>Bascanichthys</i>	C	U	U	+
<i>Caralophia</i>	C	U	U	+
<i>Dalophis</i>	C	U	U	+
<i>Ethadophis</i>	C	U	U	+
<i>Gordiichthys</i>	C	U	U	?
<i>Leptenchelys</i>	C	U	U	+
<i>Phaenomonas</i>	C	U	U	+
<b>Ophichthini</b>				
<i>Aplatophis</i>	F	B	U	-
<i>Brachysomophis</i>	C,F	U <sup>2</sup>	U	-
<i>Cirrhimuraena</i>	C	U,B	U,B	-
<i>Elapsopsis</i>	C	U	U	-
<i>Echelus</i>	C,V	M	M	-
<i>Echiophis</i>	C	B	B	-
<i>Evips</i>	C	U <sup>2</sup>	U	-
<i>Leiuranus</i>	C	U	-	
<i>Malvoliophis</i>	C	U	U	+
<i>Myrichthys</i>	M	B,M	M	+,-
<i>Mystriophis</i>	C,F	U	U	-
<i>Ophichthys</i>	C	U,B,M	U,B	+,-
<i>Ophisurus</i>	C,F	U	U	-
<i>Phyllophichthys</i>	C	U	-	
<i>Pisodonophis</i>	M	B,M	B,M	+
<i>Pogonophis</i>	C	U <sup>2</sup>	U	-
<i>Quassiremus</i>	C	U	U	-
<i>Scytalichthys</i>	C,F	U <sup>2</sup>	U	-
<i>Xyrias</i>	C	M	U	?

1. Intermaxillary teeth absent

2. Maxillary teeth biserial, dentary uniserial

Table 2. Number and Location of Branchiostegal Rays of the Species of the Ophichthidae

Counts represent the right side only. Rays joined basally are counted separately. "CH-EH" represents the cartilaginous CH-EH interspace. "Free" rays are noticeably separated from the hyoid.

	Total	Free	Along CH	CH-EH	Along EH
<i>Benthenchelys cartieri</i>	20	13	-	-	7
<i>Ahlia egmontis</i>	47	41	-	-	6
<i>Muraenichthys chilensis</i>	32	25	-	-	7
<i>Muraenichthys gymnopterus</i>	43	36	-	-	7
<i>Muraenichthys macropterus</i>	31	37	-	-	4
<i>Myrophis plumbeus</i>	43	37	-	-	6
<i>Myrophis uropterus</i>	32	26	-	-	6
<i>Myrophis vafer</i>	49	42	-	-	7
<i>Neenchelys buitendijki</i> <sup>1</sup>	30	24	-	-	6
<i>Pseudomyrophis micropinna</i>	47	40	-	-	7
<i>Pseudomyrophis nimius</i>	23	17	-	-	6
<i>Schismorhynchus labialis</i>	30	25	-	-	5
<i>Schultzidia johnstonensis</i>	33	29	-	-	4
<i>Aprognathodon platyventris</i>	28	-	14	2	12
<i>Callechelys bilinearis</i>	27	-	21	1	5
<i>Callechelys eristigmus</i>	31	-	5	6	20
<i>Callechelys galapagensis</i>	27	-	15	2	10
<i>Callechelys marmoratus</i>	29	-	18	2	9
<i>Callechelys melanotaenius</i>	29	-	12	3	14
<i>Callechelys nebulosus</i>	29	10	8	3	8
<i>Letharchus rosenblatti</i>	34	-	16	3	15
<i>Paraletharchus pacificus</i>	32	-	23	4	5
<i>Apterichthys flavicaudus</i>	16	1	1	1	13
<i>Caecula pterygera</i>	25	12	-	3	10
<i>Cirriacaecula johnsoni</i>	18	-	1	3	14
<i>Ichthyapus selachops</i>	19	-	4	2	13
<i>Lamnostoma orientalis</i>	29	26	-	-	3
<i>Stictorhinus potamius</i>	29	-	5	4	20
<i>Yirkkala lumbricoides</i>	27	-	5	2	20
<i>Yirkkala misolensis</i>	29	-	12	2	15
<i>Yirkkala tenuis</i>	25	-	4	3	18
<i>Bascanichthys panamensis</i>	30	1	5	3	21
<i>Caralophia loxochila</i>	27	-	8	4	15
<i>Phaenomonas cooperae</i>	28	19	3	5	1
<i>Phaenomonas pinnata</i>	26	19	1	6	-
<i>Aplatophis chauliodus</i>	22	-	2	1	19
<i>Brachysomophis sauropsis</i>	17	-	2	1	14
<i>Cirrhimuraena macgregori</i>	24	-	7	2	15
<i>Cirrhimuraena taeniopterus</i>	29	6	1	4	18
<i>Echelus myrus</i>	15	-	4	-	11
<i>Echelus pachyrhynchus</i>	18	-	4	1	13
<i>Echiopsis sp.</i>	21	-	4	1	16
<i>Elapsopsis cyclorhinus</i>	24	4	2	1	17
<i>Leiuranus semicinatus</i>	31	-	6	3	22
<i>Malvoliopsis pinguis</i>	21	-	4	1	16
<i>Myrichthys colubrinus</i>	30	-	22	3	5
<i>Myrichthys maculosus</i>	35	-	9	2	24
<i>Myrichthys aysstrurus</i>	31	3	3	1	24
<i>Ophichthus cephalazona</i>	27	2	2	2	21
<i>Ophichthus cruentifer</i>	17	-	4	-	13
<i>Ophichthus frontalis</i>	19	-	5	1	13
<i>Ophichthus triserialis</i>	22	-	3	-	19
<i>Ophichthus zophochir</i>	27	-	5	1	21
<i>Ophisurus serpens</i>	19	-	2	1	16
<i>Phyllophichthus xenodontus</i>	29	22	-	-	7
<i>Pisodonophis boro</i>	31	1	6	2	22
<i>Pisodonophis canerivorus</i>	30	6	1	1	22
<i>Pisodonophis daspilotus</i>	32	8	-	3	21
<i>Quassiremus nothochir</i>	21	2	2	-	18
<i>Seytalichthys mirurus</i>	25	-	4	2	19

1. From Nelson (1966a: fig. 2a)

Table 3. Gill Arch Condition in the Ophichthinae

Abbreviations are: B<sub>1-4</sub>, basibranchials; H<sub>1-3</sub>, hypobranchials; C<sub>1-5</sub>, ceratobranchials; I<sub>2-3</sub>, infrapharyngobranchials; UP<sub>3-4</sub>, upper pharyngeal dermal tooth plates; O, ossified; -0-, UP<sub>3</sub>-UP<sub>4</sub> fusion; C, cartilaginous; R, rudimentary; -, absent; \*, from Nelson (1966a: Table 1).

	B <sub>1</sub>	B <sub>2</sub>	B <sub>3</sub>	B <sub>4</sub>	H <sub>1</sub>	H <sub>2</sub>	H <sub>3</sub>	C <sub>1-4</sub>	C <sub>5</sub>	I <sub>2</sub>	I <sub>3</sub>	UP <sub>3</sub>	UP <sub>4</sub>
<i>Ophichthus zophochir</i>	O	C	R	C	O	O	C	O	O	O	O	O	O
<i>O. rhytidodermatoides</i>	O	C	-	-	O	O	C	O	O	O	O	O	O
<i>O. polyophthalmus*</i>	O	C	R	R	O	O	C	O	O	O	O	O	O
<i>O. altipinnis</i>	O	-	-	-	O	O	C	O	O	O	O	O	O
<i>O. erabo</i>	O	C	C	R	O	O	C	O	O	O	O	O	O
<i>O. cruentifer</i>	O	-	-	-	O	O	C	O	O	O	O	O	O
<i>O. cephalazona</i>	O	R	-	-	O	O	C	O	O	O	O	O	O
<i>Pisodonophis boro</i>	O	-	R	R	O	O	C	O	O	O	O	O	O
<i>P. cancrivorus</i>	O	R	C	C	O	O	C	O	O	O	O	O	O
<i>Ophisurus serpens</i>	O	C	C	C	O	O	C	O	O	O	O	O	O
<i>Evips percinctus</i>	O	C	R	R	O	O	C	O	O	O	O	O	O
<i>Echelus myrus</i>	O	C	C	C	O	O	C	O	O	O	O	O	O
<i>E. pachyrhynchus</i>	O	C	-	C	O	O	C	O	O	O	O	O	O
<i>Myrichthys colubrinus</i>	O	C	-	-	O	O	C	O	O	O	O	O	O
<i>M. maculosus</i>	O	C	-	C	O	O	C	O	O	O	O	O	O
<i>M. xysturus</i>	O	C	-	C	O	O	C	O	O	O	O	O	O
<i>Aplatophis chauliodus</i>	O	-	-	-	O	O	C	O	O	O	O	O	O
<i>Brachysomophis sawropsis</i>	O	C	-	C	O	O	C	O	O	O	O	O	O
<i>B. henshawi*</i>	O	C	-	C	O	O	C	O	O	O	O	O	O
<i>Cirrhimuraena macgregori</i>	O	C	R	R	O	O	C	O	O	O	O	O	O
<i>C. taeniopterus</i>	O	-	R	-	O	O	C	O	O	O	O	O	O
<i>Echiophis intertinctus*</i>	O	R	R	C	O	O	C	O	O	O	O	O	O
<i>Echiophis</i> sp.	O	C	C	C	O	O	C	O	O	O	O	-0-	-0-
<i>Xyrias revulsus</i>	O	C	-	C	O	O	C	O	O	O	O	-0-	-0-
<i>Malvoliophis pinguis</i>	O	C	R	R	O	O	C	O	O	O	O	-0-	-0-
<i>Elapsopsis cyclorhinus</i>	O	C	R	-	O	O	C	O	-	O	O	-0-	-0-
<i>Leiuranus semicinctus</i>	O	C	-	C	O	O	C	O	-	O	O	-0-	-0-
<i>Phyllophichthus xenodontus</i>	O	C	R	-	O	O	C	O	-	O	O	O	O
<i>Pogonophis fossatus</i>	O	C	-	-	O	O	C	O	-	O	O	O	O
<i>Quassiremus evionthas</i>	O	-	-	-	O	O	C	O	-	O	O	O	O
<i>Q. nothochir</i>	O	-	-	-	O	O	C	O	-	O	O	O	O
<i>Dalophis imberbis</i>	O	C	C	R	O	O	C	O	O	O	O	O	O
<i>Bascanichthys teres*</i>	O	C	-	C	O	O	C	O	O	O	O	O	O
<i>B. panamensis</i>	O	-	-	C	O	O	C	O	-	O	O	O	O
<i>Allips concolor</i>	O	C	-	C	O	O	C	O	-	O	O	O	O
<i>Etheadophis byrnei</i>	O	C	-	-	O	O	C	O	-	O	O	O	O
<i>E. merenda</i>	O	C	R	C	O	O	C	O	-	O	O	O	O
<i>Phaenomonas pinnata</i>	O	C	-	C	O	O	C	O	-	O	O	O	O
<i>Caralophia loxochila</i>	O	-	C	C	O	O	C	O	-	O	O	-0-	-0-
<i>Callechelys marmoratus</i>	O	C	-	-	O	O	C	O	-	O	O	O	O
<i>Aprognathodon platyventris</i>	O	C	-	-	O	O	C	O	-	O	O	O	O
<i>Paraletarchus pacificus</i>	O	C	-	R	O	O	C	O	-	O	O	O	O
<i>Letharchus velifer*</i>	O	C	-	R	O	O	C	O	-	O	O	O	O
<i>Letharchus rosenblatti</i>	O	C	-	R	O	O	C	O	-	O	O	O	O
<i>Ichthyapus selachops</i>	O	-	-	C	O	O	C	O	O	O	O	O	O
<i>Cirriacaecula johnsoni</i>	O	-	-	R	O	O	C	O	O	O	O	-0-	-0-
<i>Apterichtus flavicaudus</i>	O	-	-	-	O	O	C	O	-	O	O	O	O
<i>Caecula pterygera</i>	O	C	C	C	O	O	C	O	-	O	O	O	O
<i>Yirrkala lumbricoides</i>	O	C	C	C	O	O	C	O	-	O	O	O	O
<i>Y. tenuis</i>	O	R	C	C	O	O	C	O	-	O	O	O	O
<i>Y. misolensis</i>	O	C	C	C	O	O	C	O	-	O	O	O	O
<i>Y. kaupi</i>	O	C	C	C	O	O	C	O	-	O	O	O	O
<i>Larnostoma orientalis</i>	O	C	-	-	O	O	C	O	-	O	O	O	O
<i>Stictorhinus potamius</i>	O	C	C	C	O	O	C	O	-	O	O	O	O

Table 4. Gill Arch Condition in the Myrophinae

Abbreviations as in Table 3.

	B <sub>1</sub>	B <sub>2</sub>	B <sub>3</sub>	B <sub>4</sub>	H <sub>1</sub>	H <sub>2</sub>	H <sub>3</sub>	C <sub>1-4</sub>	C <sub>5</sub>	I <sub>2</sub>	I <sub>3</sub>	UP <sub>3</sub>	UP <sub>4</sub>
<i>Benthenchelys cartieri</i>	C	-	-	-	0	0	0	0	-	0	0	-0-	
<i>Ahlia egmontis</i>	0	-	-	-	0	0	-	0	-	-	0	0	0
<i>Myrophis punctatus</i> *	0	R	-	-	0	0	C	0	-	0	0	0	0
<i>M. vafer</i>	0	-	-	-	0	0	C	0	-	0	0	0	0
<i>M. uropterus</i>	0	-	-	-	0	0	C	0	-	0	0	0	0
<i>M. plumbeus</i>	0	-	-	-	0	0	C	0	-	0	0	-0-	
<i>Pseudomyrophis nimius</i>	0	-	-	-	0	0	C	0	-	0	0	0	0
<i>P. micropinna</i>	0	C	-	-	0	0	C	0	-	0	0	0	0
<i>Neenchelys buitendijki</i> *	R	-	-	-	0	0	C	0	-	0	0	0	0
<i>Schultzia johnstonensis</i>	-	-	-	-	0	0	C	0	-	-	0	-0-	
<i>Schismorhynchus labialis</i>	-	-	-	-	0	0	-	0	-	-	0	-0-	
<i>Muraenichthys chilensis</i>	-	-	-	-	0	0	C	0	-	0	0	0	0
<i>M. macropterus</i>	-	-	-	-	0	0	C	0	-	C	0	0	0
<i>M. cookei</i> *	-	-	-	-	0	0	C	0	-	C	0	0	0
<i>M. gymnotus</i>	-	-	-	-	0	0	C	0	-	-	0	0	0
<i>M. laticaudata</i>	-	-	-	-	0	0	C	0	-	0	0	0	0
<i>M. schultzei</i>	-	-	-	-	0	0	C	0	-	-	0	-0-	
<i>M. gymnopterus</i>	-	-	-	-	0	0	C	0	-	-	0	-0-	

Table 5. Lateral Line and Cephalic Pore Conditions in Ophichthine Genera and Subgenera

Cephalic pore locations are illustrated in Figure 24. Abbreviations are: \*, condition of type species unknown; +, present; -, absent; C, lateral line ossicles continuous; M, lateral line ossicles moderately separated at pores; S, lateral line ossicles separated at pores.

	tp <sup>2</sup>	pop <sup>3</sup>	pop <sup>4</sup>	Lateral Line Ossicles
<i>Ophichthus</i>	-	+	-	S
<i>Echelus</i>	-	+	-	S
<i>Ophisurus</i>	-	+	-	S
<i>Pisodonophis</i>	-	+	-	S
<i>Quassiremus</i>	-	+	-	S
<i>Cirrhimuraena</i> *	-	+	-	S
<i>Calamuraena</i>	?	+	-	?
<i>Jenkinsiella</i>	-	-	-	S
<i>Echiophis</i>	-	+	-	S
<i>Mystriophis</i>	-	+	-	S
<i>Aplatophis</i>	-	-	-	S
<i>Brachysomophis</i> *	-	-	-	S
<i>Xyrias</i>	-	-	-	?
<i>Seytalichthys</i>	-	-	-	S
<i>Pogonophis</i>	-	-	-	M
<i>Eviops</i>	-	-	-	M
<i>Leturanus</i>	-	-	-	M
<i>Elapsopsis</i>	-	-	-	M
<i>Phyllophichthus</i>	-	-	-	S
<i>Malvoliophis</i>	-	-	-	M
<i>Myrichthys</i>	-	-	-	M
<i>Apteriichtus</i>	+,-	+	+,-	C
<i>Ichthyapus</i>	+	+	+,-	C
<i>Cirriacaecula</i>	+	+	+	C
<i>Stictorhinus</i>	+	+	-	C
<i>Caecula</i>	+	+	-	C
<i>Yirrkala</i>	+,-	-	-	C
<i>Lamnostoma</i>	-	-	-	C
<i>Aprognathodon</i>	-	-	-	C
<i>Callecheilus</i>	-	-	-	C
<i>Letharchus</i>	-	-	-	C
<i>Leuropharus</i>	-	-	-	C
<i>Paraletharchus</i>	-	-	-	C
<i>Bascaniichthys</i> *	-	-	-	M
<i>Allips</i>	-	-	-	M
<i>Phaenomonas</i>	-	-	-	M
<i>Ethadophis</i>	-	-	-	M
<i>Caralophia</i>	-	-	-	S
<i>Leptenchelys</i>	-	-	-	?
<i>Dalophis</i>	-	-	-	M



Table 6. Vertebral Counts of Various Ophichthid Species

Data were obtained during the present study except as cited. The listing is arranged alphabetically by genus and species within each tribe. Counts include the hypural. "N" indicates number of individuals.

	Holotype	Range	Mean	N	Source
<i>Benthenchelys cartieri</i>		156-174	168.3	34	Castle, 1972
<i>Ahlia egmontis</i>			152	1	
<i>Muraenichthys aoki</i>	137				
<i>Muraenichthys australis</i>			152		Castle, 1965
<i>Muraenichthys breviceps</i>			164		Castle, 1965
<i>Muraenichthys chilensis</i>	149	148-153	150.9	12	McCosker, 1970
<i>Muraenichthys cooki</i>			130		Gosline, 1951a
<i>Muraenichthys gymnotus</i>		129-130	129.5	2	
<i>Muraenichthys hattae</i>	154				
<i>Muraenichthys iredalei</i>		126-127	126.5	2	
<i>Muraenichthys macropterus</i>		127-130	128.2	4	
<i>Muraenichthys schultzei</i>			122	2	
<i>Muraenichthys thompsoni</i>	128?	128-133	130.5	2	
<i>Myrophis plumbeus</i>		142-154			Blache, et al., 1970
<i>Myrophis punctatus</i>		138-145			Eldred, 1966
<i>Myrophis vafer</i>		146-150	147.8	5	
(holotype of <i>Hesperomyrus fryi</i> )	154?				
<i>Neenchelys buitendijki</i>		145-148			Mohamed, 1958
<i>Pseudomyrophis micropinna</i>	174				
<i>Pseudomyrophis nimius</i>		212-216	214	2	
<i>Schismorhynchus labialis</i>	136	134-138	136	6	
<i>Schultziidia johnstonensis</i>		145-149	151.2	5	
<i>Schultziidia retropinnis</i> (holotype of <i>Muraenichthys malaita</i> )	133				
<i>Aprognathodon platyventris</i>		150-155	152.5	2	
<i>Callechelys bilinearis</i>		161-163	162	2	
<i>Callechelys cliffi</i>	155	149-158	154.9	14	
<i>Callechelys eristigmus</i>	159	154-163	157.9	30	
<i>Callechelys galapagensis</i>	172	170-174	172	4	
<i>Callechelys holochromus</i>	166				
<i>Callechelys leucopterus</i>		162-165	164	4	Blache and Cadenat, 1971
<i>Callechelys marmoratus</i>		176-183	179	4	
(holotype of <i>Callechelys guichenoti</i> )	183				
<i>Callechelys melanotaenius</i>		200-205	203	5	
<i>Callechelys muraena</i>	141	141-144	142.5	2	
<i>Callechelys nebulosus</i>		158-159	158.7	3	
<i>Callechelys perryae</i>	178				Blache and Cadenat, 1971
<i>Callechelys springeri</i>	170	166-170	168	2	
<i>Callechelys striatus</i>			192	1	
<i>Letharchus velifer</i>	139	135-143	139.5	14	McCosker, 1974
<i>Letharchus rosenblatti</i>	151	144-151	148.4	20	McCosker, 1974
<i>Leuropharus lasiops</i>	135				
<i>Paraletarchus opercularis</i>	180	171-180	174.7	9	
<i>Paraletarchus pacificus</i>	166	156-167	160.4	15	
<i>Apteriichtus ansp</i>		123-132		-	Böhlke, 1968
<i>Apteriichtus caecus</i>			151	1	
<i>Apteriichtus equatorialis?</i> <sup>1</sup> (holotype has 53 preanal vertebrae)			146	1	
<i>Apteriichtus flavicaudus</i>		145-157	149.6	5	
<i>Apteriichtus gymnoceclus</i>			136	1	
<i>Apteriichtus kendalli</i>		137-144			Böhlke, 1968
<i>Apteriichtus klazingai</i>	140				
<i>Caecula pterygera</i>	126	126-130	128.6	8	Böhlke and McCosker, 1975
<i>Cirriacaecula johnsoni</i>			119	1	
<i>Ichthyapus acutirostris</i>					Blache and Bauchot, 1972
<i>Ichthyapus ophioneus</i>	133	132-137	133.7	3	
<i>Ichthyapus selachops</i>		137-144	139.3	15	

1. The holotype of *Caecula equatorialis* Myers and Wade lacks a tail. The specimen recorded here, ANSP 117436, is from 3°15'S, 80°19'W, and was not compared with the type.

Table 6. Continued

	Holotype	Range	Mean	N	Source
<i>Ichthyapus vulturis</i> <sup>2</sup>	123				
from Palau, Tahiti, and Seychelles		117-127	121.8	12	
from Hawaii and Kure		120-124	122.2	4	
from Easter Island		130-134	132.3	9	
<i>Lammostoma kampeni</i>			143	1	
<i>Lammostoma mindora</i>	144				
<i>Lammostoma orientalis</i>		134-137	135.3	3	
<i>Lammostoma philippinensis</i>	153 <sup>3</sup>				
<i>Stictorhinus potamius</i>	140	135-142	139.4	11	Böhlke and McCosker, 1975
<i>Yirrkala lumbrioides</i>		151-154	152.5	2	
(paratype of <i>Yirrkala chaselingi</i> )			153		
<i>Yirrkala tenuis</i>			153	1	
<i>Allips concolor</i>	174				
<i>Bascanichthys cecilae</i>	226	225-226	225.5	2	Blache and Cadenat, 1971
<i>Bascanichthys congoensis</i>	189	189-190	189.5	2	Blache and Cadenat, 1971
<i>Bascanichthys longissimus</i>			212	-	Blache and Cadenat, 1971
<i>Bascanichthys myersi</i>	215				
<i>Bascanichthys panamensis</i>			181	1	
<i>Bascanichthys paulensis</i>	191				
<i>Bascanichthys tenuis</i>	203				
<i>Bascanichthys teres</i>		181-184		-	Blache and Cadenat, 1971
<i>Caralophia lowoehila</i>		139-145	142.3	3	
<i>Dalophis imberbis</i>	152	148-159	152.2	14	Blache and Bauchot, 1972
<i>Etheadophis byrnei</i>	189				
<i>Etheadophis merenda</i>	159				
<i>Leptenchelys vermiformis</i>	163				
<i>Phaenomonas cooperae</i>	270	243-270	256	8	
<i>Phaenomonas pinnata</i>	187	175-194	186.5	14	
<i>Aplatophis chauliodus</i>		110-111	110.5	2	
<i>Brachysomophis henshawi</i>			130	-	Gosline, 1951a
<i>Brachysomophis sauropsis</i>		119-125	121	4	
<i>Cirrhimuraena macgregori</i>			181	-	Gosline, 1951a
<i>Cirrhimuraena taeniopterus</i>			183	1	
<i>Echelus myrus</i>					
from the Mediterranean		151-155		-	Grassi, 1913
from the eastern tropical Atlantic		149-152		-	Blache, et al., 1970
<i>Echelus pachyrhynchus</i>	157	149-157		-	Blache, 1968
<i>Echiophis intertinctus</i>	132	132-143		-	Blache, 1971
<i>Echiophis mordax</i>			130		
<i>Echiophis</i> sp. <sup>3</sup>		132-139	135.6	14	
<i>Elapsopsis cyclorhinus</i>		153-160	156.5	2	
<i>Evips percinctus</i>	132				
<i>Leiuranus semicinctus</i>		162-169	166.3	3	
(holotype of <i>Machaerenchelys phoenixensis</i> )	170				
<i>Myrichthys bleekeri</i>			196	1	
<i>Myrichthys colubrinus</i>		197-201	199	2	
<i>Myrichthys maculosus</i>					
from Hawaii and Midway		174-182	178.5	16	
from western Pacific		190-199	193.2	10	
<i>Myrichthys ocellatus</i>		170-171	170.5	2	
<i>Myrichthys pardalis</i>	158	151-159		-	Blache and Cadenat, 1971
<i>Myrichthys xystrurus</i>		149-163	152.5	20	
<i>Mystriophis blastorhinus</i>	142				Blache, 1971
<i>Mystriophis crozieri</i>		136-144	140.7	57	Blache, 1971
<i>Mystriophis rostellatus</i>		154-158	155.5	13	Blache, 1971
<i>Ophichthus altipinnis</i>			173	1	
<i>Ophichthus callaensis</i>			153	1	
<i>Ophichthus cruentifer</i>			146	1	
<i>Ophichthus erabo</i>	155		155	2	
<i>Ophichthus frontalis</i>		144-157	149.4	7	
<i>Ophichthus gomesi</i>			141	-	Jordan and Davis, 1892

2. Population differences in *Ichthyapus vulturis* are treated in Randall and McCosker (1974).
3. An undescribed species ranging from the Gulf of California to Panama.

Table 6. Continued

	Holotype	Range	Mean	N	Source
<i>Ophichthus macrochir</i>			144	-	Castle, 1965
<i>Ophichthus ocellatus</i>			134	-	Jordan and Davis, 1892
<i>Ophichthus ophis</i>					
from Brazil			162	1	
from eastern tropical Atlantic		161-170		-	Blache, in litt.
<i>Ophichthus rhytidodermatoides</i>			191	1	
<i>Ophichthus triserialis</i>		145-160	152.5	2	
<i>Ophichthus wiserialis</i>	152?				
<i>Ophichthus urolophus</i>			136	1	
<i>Ophichthus zophochir</i>		150-152	150.7	3	
<i>Ophisurus serpens</i>		200-208			Blache, in litt.
<i>Phyllophichthus xenodontus</i>		169-170	169.5	6	
<i>Pisodonophis boro</i>		171-173	172	2	
<i>Pisodonophis canerivorus</i>			155	1	
<i>Pisodonophis daspilatus</i>	137?	137-138	137.5	2	
<i>Pogonophis fossatus</i>		166-171	168.5	2	
<i>Quassiremus evionthas</i>			153	1	
<i>Quassiremus nothochir</i>		139-142	140.8	4	
<i>Scytalichthys miurus</i>		143-149	146	4	
<i>Xyrias revulsus</i>	158				

Table 7. Characteristics of the Ophichthidae and Related Eel Families

Abbreviations are: F, fused; O, ossified; R, reduced; S, sutured; +, present; -, absent. Data are from this study and various sources, including McAllister (1968), Robins and Robins (1970, 1971), and Smith and Castle (1972).

	Frontal Condition	Frontal Commissure	Temporal Pore Canal	Gill Arch Ossification	Branchiostegal Rays (pairs)
Ophichthidae	F	+	+		
Ophichthinae				O	15-34
Myrophinae				R	20-49
Congridae	F	-	+	O	8-17
Muraenesocidae	F	-	+?	O	8-22
Macrocephenchelyidae	F	-	+	O	8
Dysommidae	F	-	-	R	9-16
Xenocongridae	S	-	+	R	12-21
Heterenchelyidae	S	-	+	O	11-14
Muraenidae	S	-	-	R	<10
Anguillidae	S	-	+	O	8-14

Table 8. Morphological and Meristic Characters of the Species of *Callechelyini*

Adapted from and expanded upon McCosker and Rosenblatt (1972, Table 5). Abbreviations are as follows:  $\Delta$ , rounded mean value; \*, from the holotype; +, present; -, absent; ?, condition not known. Postanal lengths in thousandths of total length.

	Postanal <sup><math>\Delta</math></sup> Length	Vertebrae	Scapula	Urohyal	Branchiostegal Rays	Epihyal Ray Broadening
<i>Aprognathodon platyventris</i>	351	155 <sup><math>\Delta</math></sup>	+	simple	28	extreme
<i>Leuropharus lasiops</i>	405	135*	+	?	32?	no?
<i>Letharchus velifer</i>	400	149*	+	?	32	extreme
<i>L. rosenblatti</i>	428	151*	+	simple	34	extreme
<i>Paraletarchus pacificus</i>	352	166*	+	simple	32	yes
<i>P. opercularis</i>	392	180*	+	simple	30	yes
<i>Callechelys nebulosus</i>	408	159 <sup><math>\Delta</math></sup>	+	simple	29	yes
<i>C. springeri</i>	350	170*	+	simple	25?	yes
<i>C. bilinearis</i>	364	162 <sup><math>\Delta</math></sup>	+	forked	27	no
<i>C. cliffi</i>	434	155*	+	forked	26	no
<i>C. galapagensis</i>	444	172*	+	forked	27	no
<i>C. luteus</i>	415	213	+	forked	27	no
<i>C. muraena</i>	385	141*	+	forked	23?	no
<i>C. marmoratus</i>	345	180 <sup><math>\Delta</math></sup>	-	simple	29	no
<i>C. eristigmus</i>	295	158*	-	simple	31	no
<i>C. melanotaenius</i>	282	203 <sup><math>\Delta</math></sup>	-	simple	29	no
<i>C. striatus</i>	304	192	-	simple	26	no
<i>C. perryae</i>	319	178*	-	simple	24	no
<i>C. leucopterus</i>	453	164 <sup><math>\Delta</math></sup>	?	?	?	?
<i>C. holochromus</i>	333	166*	-	simple	?	yes
<i>C. bitaeniatus</i>	385	?	?	?	?	?

Table 9. Characteristics of the Species of *Callechelyini* Used in Programs REGROUP and WVGM

---

1. Meristics	
Vertebrae:	130-139; 140-149; 150-159; 160-169; 170-179; 180-189; 190-199; 200-209; 210-219
Branchiostegal rays:	22-23; 24-25; 26-27; 28-29; 30-31; 32-33; 34-35
Supraorbital pores:	3 or 4
II. External Morphology	
Postanal length:	275-299; 300-324; 325-349; 350-374; 375-399; 400-424; 425-449; 450-474
Anal fin:	present or absent
Gill opening "pocket":	present or absent
Underside of snout:	grooved, slightly grooved or ungrooved
Snout:	blunt or conical; papillate or smooth
Anterior nostril:	tubular or not tubular
III. Internal Morphology	
DF0:	above supraoccipital or above epiotics
Neurocranium:	rounded or depressed
Intermaxillary teeth:	present or absent
Urohyal:	forked, simple and cartilaginous or simple and ossified
Hyoid:	inflexible along CH-EH suture, slightly flexible or well separated
Hypohyals:	present or absent
Vomerine teeth:	present or absent
Scapula (?):	present or absent
Epihyal rays:	broadened basally, moderately broadened or slender
Third hypobranchial:	ossified or cartilaginous
IV. Coloration	
	Mottled or weakly spotted
	Strongly spotted
	Longitudinally banded
	Uniform body (fins may contrast)

---

Table 10. Distribution of Certain Ophichthid Genera

Refer to text for discussion of those genera marked with an asterisk.

---

I. Circumtropical		
<i>Apterichtus</i> <i>Ichthyapus</i>	<i>Bascanichthys</i> <i>Myrichthys</i> <i>Ophichthus</i>	<i>Callechelys</i> <i>Myrophis</i>
II. Restricted to Indo-Pacific		
<i>Achirophichthys</i> <i>Brachysomophis</i> <i>Cirri caecula</i> <i>Lamostoma</i> <i>Muraenichthys*</i> <i>Schulzidia</i>	<i>Allips</i> <i>Caecula</i> <i>Elapsopsis</i> <i>Leiruanus</i> <i>Neenchelys</i> <i>Xyrias</i>	<i>Benthenchelys</i> <i>Cirrhimuraena</i> <i>Evips</i> <i>Malvoliophis</i> <i>Schismorhynchus</i> <i>Yirrkala</i>
III. Restricted to New World		
<i>Echiophis*</i>	<i>Letharchus</i> <i>Quassiremus</i>	<i>Pseudomyrophis</i>
IV. Restricted to Eastern Pacific		
<i>Ethadophis</i> <i>Paralatharchus</i>	<i>Leptenchelys</i> <i>Pogonophis</i>	<i>Leuropharus</i> <i>Scytalichthys</i>
V. Restricted to Western Atlantic		
<i>Ahlia</i> <i>Gordichthys</i>	<i>Aprognathodon</i> <i>Stictorhinus</i>	<i>Caralophia</i>
VI. Restricted to Eastern Atlantic and Mediterranean		
<i>Dalophis</i>	<i>Echelus</i>	<i>Mystriophis</i>

---

## INDEX TO GENERA AND SPECIES

(Included are recognized species and valid and invalid genera)

- Acanthenchelys* 80,81  
*Achirophichthys* 65  
*acuminatus*, *Myrichthys* 78  
*acutirostris*, *Ichthyapus* 67,68  
*acutirostris*, *Muraenichthys* 59  
*Ahlia* 58  
*aliculatus*, *Letharchus* 64  
*Allips* 70  
*altipinnis*, *Ophichthus* 80,81  
*Anepistomon* 82  
*anguiformis*, *Apterichthys* 66  
*Anguisurus* 68  
*ansp*, *Apterichthys* 66  
*Antobranchia* 80  
*Aotea* 58,59  
*apicalis*, *Ophichthus* 80,81  
*Aplatophis* 74  
*Aprognathodon* 62  
*Apterichthys* 59,65,68  
*asakusae*, *Ophichthus* 81  
*ascensionsis*, *Ophichthus* 81  
*ater*, *Ophichthus* 81  
*atlanticus*, *Brachysomophis* 74  
*australis*, *Muraenichthys* 58,59  
*australis*, *Myrophis* 60  
*Bascanichthys* 70,78  
*bascanoides*, *Bascanichthys* 71  
*Benthenchelys* 57,85  
*bilinearis*, *Callechelys* 63  
*bitaeniatus*, *Callechelys* 63  
*blastorhinos*, *Echiophis* 77,79  
*bleekeri*, *Myrichthys* 78  
*bonaparti*, *Ophichthus* 80,81  
*boro*, *Pisodonophis* 82  
*boulengeri*, *Dalophis* 72  
*Brachycheirophis* 83  
*Brachysomophis* 65,74,75,79  
*Branderius* 65  
*breviceps*, *Muraenichthys* 59  
*buitendijki*, *Neenchelys* 60  
*byrnei*, *Ethadophis* 72  
*Caecilia* 65  
*Caecula* 63,65,66,67,69,70,72,85  
*caecus*, *Apterichthys* 65,66  
*Calamuraena* 75  
*calamus*, *Cirrhimuraena* 75  
*Callechelys* 62,72  
*callaensis*, *Ophichthus* 81  
*cancrivorus*, *Pisodonophis* 82,83  
*Caralophia* 71  
*cartieri*, *Benthenchelys* 57  
*ceciliae*, *Bascanichthys* 71  
*celebicus*, *Ophichthus* 81  
*Centrurophis* 79,81  
*cephalopeltis*, *Dalophis* 71,72  
*cephalozona*, *Ophichthus* 79,80,81  
*chauiodius*, *Aplatophis* 74  
*cheilopogon*, *Cirrhimuraena* 75  
*cheni*, *Myrophis* 60  
*chilensis*, *Muraenichthys* 59  
*chinensis*, *Cirrhimuraena* 75  
*Chlevastes* 78  
*Cirrhimuraena* 75,85  
*cirrocheilos*, *Brachysomophis* 74,75  
*Cirricaecula* 59,67,68  
*cliffi*, *Callechelys* 63  
*Coecilophis* 80,81  
*Cogrus* 79,81  
*colubrinus*, *Myrichthys* 78  
*concolor*, *Allips* 70  
*congoensis*, *Bascanichthys* 71  
*cookei*, *Muraenichthys* 59  
*cooperae*, *Phaenomonas* 73  
*copelandi*, *Pisodonophis* 82  
*crocodilinus*, *Brachysomophis* 65,74  
*crosnieri*, *Mystriophis* 79  
*Crotalopsis* 76,77  
*cruentifer*, *Ophichthus* 80,81,82  
*Cryptopterenchelys* 80  
*Cryptopterus* 80,81  
*Cryptopterygium* 62,63  
*Cyclophichthys* 77  
*cyclorhinus*, *Elapsopsis* 77  
*cylindricus*, *Bascanichthys* 71  
*cylindroideus*, *Myrophis* 59,60  
*Dalophis* 62,68,71  
*daspilotus*, *Pisodonophis* 82,83  
*derbeyensis*, *Ophichthus* 81  
*devisi*, *Muraenichthys* 59  
*dromicus*, *Pisodonophis* 82  
*Echelus* 75,76,81,85  
*Echiophis* 76,77,79  
*Echiopsis* 76  
*egmontis*, *Ahlia* 58  
*Elapsopsis* 77  
*epinepheli*, *Apterichthys* 66  
*episcopus*, *Ophichthus* 81  
*equatorialis*, *Apterichthys* 66  
*erabo*, *Ophichthus* 81  
*eristigmus*, *Callechelys* 63  
*Ethadophis* 72  
*evermanni*, *Ophichthus* 81  
*evionthas*, *Quassiremus* 83,84



- Evips* 77  
*ilaria*, *Bascanichthys* 71  
*flavicaudus*, *Apterichthys* 68  
*foresti*, *Apterichthys* 65,66  
*fossatus*, *Pogonophis* 83  
*frio*, *Myrophis* 60  
*frontalis*, *Ophichthys* 81  
*fusca*, *Yirrkala* 69  
*galapagensis*, *Callechelys* 63  
*garretti*, *Ophichthys* 81  
*Gisenchelys* 80,81  
*gjellerupi*, *Yirrkala* 69  
*godeffroyi*, *Muraenichthys* 59  
*gomesi*, *Ophichthys* 80,81  
*Gordiichthys* 63,72  
*gracilis*, *Apterichthys* 65  
*grandoculis*, *Ophichthys* 81  
*gymnocelus*, *Apterichthys* 66  
*gymnopterus*, *Muraenichthys* 58,59  
*gymnotus*, *Muraenichthys* 59  
*hattae*, *Muraenichthys* 59  
*Hemerorhinus* 67,70  
*henshawi*, *Brachysomophis* 75  
*Herpetoichthys* 80  
*Hesperomyrus* 59  
*heyningi*, *Hemerorhinus* 67  
*hijala*, *Pisodonophis* 82  
*hoevenii*, *Pisodonophis* 82  
*holochromus*, *Callechelys* 62,63  
*hypselopterus*, *Pisodonophis* 82  
*Ichthyapus* 59,66,67,68  
*imberbis*, *Dalophis* 71,72  
*inhacae*, *Cirrhimuraena* 75  
*Innominado* 79,81  
*intertinctus*, *Echiophis* 76,77  
*iredalei*, *Muraenichthys* 59  
*irretitus*, *Gordiichthys* 72  
*Jenkinsiella* 75,85  
*johnsoni*, *Cirricaecula* 64  
*johnstonensis*, *Schultzia* 61,62  
*kampeni*, *Lamnostoma* 65  
*kaupi*, *Yirrkala* 69,70  
*kendalli*, *Apterichthys* 65  
*kirkii*, *Bascanichthys* 71  
*klazingai*, *Apterichthys* 66  
*labialis*, *Schismorhynchus* 61  
*Lamnostoma* 65,67,68,69,85  
*lasiops*, *Leuropharus* 64  
*laticaudata*, *Muraenichthys* 58,59  
*Lejuranus* 77  
*Leptenchelys* 72,73,85  
*Leptognathus* 82  
*Leptorhinophis* 80  
*Leptorhynchus* 82  
*lepturus*, *Myrophis* 60  
*Letharchus* 63,64  
*leucopterus*, *Callechelys* 63  
*Leuropharus* 64  
*limkouensis*, *Ophichthys* 81  
*longissimus*, *Bascanichthys* 71  
*loxochila*, *Caralophia* 71  
*lumbricoides*, *Yirrkala* 69,70  
*luteus*, *Callechelys* 63  
*macgregori*, *Cirrhimuraena* 75  
*Machaerenchelys* 77  
*macrochir*, *Ophichthys* 81  
*macrodon*, *Yirrkala* 69  
*Macrodonophis* 76  
*macrops*, *Ophichthys* 81  
*macropterus*, *Muraenichthys* 59  
*macrorhynchus*, *Ophisurus* 82  
*macrostomus*, *Muraenichthys* 59  
*macrurus*, *Phyllophichthys* 82  
*maculata*, *Yirrkala* 69  
*maculatus*, *Ophichthys* 79,81  
*maculosus*, *Myrichthys* 78,79  
*madagascariensis*, *Ophichthys* 81  
*magnioculis*, *Ophichthys* 80,81  
*Malvoliophis* 77,78,85  
*manilensis*, *Ophichthys* 81  
*marginatus*, *Ophichthys* 81  
*marmoratus*, *Callechelys* 62,63  
*melanochir*, *Ophichthys* 81  
*melanoporus*, *Ophichthys* 81  
*melanotaenius*, *Callechelys* 63  
*merenda*, *Etheadophis* 72  
*Microdonophis* 75,80,81,85  
*micipinna*, *Pseudomyrophis* 60,61  
*Microrhynchus* 65-66  
*microtretus*, *Neeenchelys* 60  
*mindora*, *Lamnostoma* 69  
*misolensis*, *Yirrkala* 69,70  
*miurus*, *Scytalichthys* 84  
*moluccensis*, *Yirrkala* 69  
*monodi*, *Apterichthys* 66  
*mordax*, *Echiophis* 76,77  
*moseri*, *Apterichthys*  
*multidentatus*, *Dalophis* 72  
*multiserialis*, *Ophichthys* 81,82  
*muraena*, *Callechelys* 63,65  
*Muraenichthys* 58,59,61,62,73  
*Muraenophis* 80  
*Muraenopsis* 80,81  
*myersi*, *Bascanichthys* 71  
*Myrichthys* 78,79  
*Myrophis* 57,58,59  
*Myroptera* 58  
*Myrus* 75,76

- myrus*, *Echelus* 75  
*Mystriophis* 77,79,84  
*natalensis*, *Yirrkala* 69  
*nebulosus*, *Callechelys* 63  
*Neenchelys* 60,85  
*nimius*, *Pseudomyrophis* 60,61  
*nothochir*, *Quassiremus* 84  
*obtusirostris*, *Dalophis* 72  
*oculatus*, *Myrichthys* 78  
*oliveri*, *Cirrhimuraena* 75  
*omanensis*, *Ichthyapus* 68  
*Omochelys* 80,81,82,85  
*opercularis*, *Paraetharchus* 64  
*Ophichthus* 69,73,75,76,79,80,81,82,83,85  
*ophioneus*, *Ichthyapus* 67,68  
*Ophis* 79,80,81  
*Ophisuraphis* 65  
*Ophisurapus* 65  
*Ophisurus* 74,76,77,78,79,80,81,83  
*Ophithorax* 79,81  
*opici*, *Hemerorhinus* 67  
*orientalis*, *Lamnostoma* 68,69  
*Oxydontichthys* 80  
*pachyrhynchus*, *Echelus* 76  
*pacificus*, *Ophichthus* 81  
*pacificus*, *Paraetharchus* 64  
*panamensis*, *Bascanichthys* 71  
*Pantonora* 69,70  
*Paraetharchus* 64  
*Paramyrus* 59  
*pardalis*, *Myrichthys* 79  
*parilis*, *Ophichthus* 81  
*paucidens*, *Cirrhimuraena* 75  
*paulensis*, *Bascanichthys* 71  
*Pelia* 71,72  
*percinctus*, *Evips* 77  
*perryae*, *Callechelys* 63  
*Phaenomonas* 61,73  
*philippinensis*, *Muraenichthys* 59  
*Phyllophichthus* 78,82  
*pictum*, *Lamnostoma* 67,68  
*pinguis*, *Malvoliophis* 78  
*pinnata*, *Phaenomonas* 73  
*Pisodonophis* 79,80,81,82,83,85  
*platyrhynchus*, *Myrophis* 60  
*platyventris*, *Aprognathodon* 62  
*playfairi*, *Cirrhimuraena* 75  
*plumbeus*, *Myrophis* 59,60  
*Poecilocephalus* 79,81  
*Pogonophis* 83  
*polyophthalmus*, *Ophichthus* 81  
*porphyreus*, *Mystriophis* 79  
*potamius*, *Stictorhinus* 69  
*productus*, *Quassiremus* 84  
*Pseudomyrophis* 60,61  
*Pterurus* 71  
*pterygera*, *Caecula* 66  
*punctatus*, *Myrophis* 59,60  
*puncticeps*, *Ophichthus* 80,81  
*punctifer*, *Echiophis* 76,77  
*pusillus*, *Bascanichthys* 71  
*Quassiremus* 83  
*reguis*, *Ophichthus* 81  
*remiger*, *Ophichthus* 81  
*retifer*, *Ophichthus* 81  
*retropinna*, *Schultzidia* 81  
*retropinnis*, *Ophichthus* 62  
*revulsus*, *Xyrias* 84  
*Rhinenchelys* 67,68  
*rosenblatti*, *Letharchus* 64  
*roseus*, *Ophichthus* 81  
*rostellatus*, *Mystriophis* 79  
*rufus*, *Ophichthus* 81  
*rutidoderma*, *Ophichthus* 81  
*rutidodermatoides*, *Ophichthus* 81  
*sauropsis*, *Brachysomophis* 75  
*Schismorhynchus* 59,61  
*schultzei*, *Muraenichthys* 59  
*Schultzidia* 59,61  
*Scolecenchelys* 58,59  
*Scytalichthys* 84  
*Scytallurus* 71  
*Scytalophis* 80,81  
*selachops*, *Ichthyapus* 68  
*semicinctus*, *Leiuranus* 77,78  
*semicinctus*, *Pisodonophis* 82  
*serpens*, *Ophisurus* 81,82  
*sibogae*, *Muraenichthys* 59  
*Sphagebranchus* 65,66,67,68,69,70,71,72,77  
*spinicauda*, *Ophichthus* 80,81  
*springeri*, *Callechelys* 63,72  
*stenopterus*, *Ophichthus* 81  
*Stethopterus* 77  
*Stictorhinus* 69  
*striatus*, *Callechelys* 63  
*Syletophis* 80  
*Syletor* 80  
*taeniopterus*, *Cirrhimuraena* 75  
*taylori*, *Lamnostoma* 69  
*tenuis*, *Bascanichthys* 71,73  
*tenuis*, *Yirrkala* 69  
*teres*, *Bascanichthys* 70,71  
*thompsoni*, *Muraenichthys* 59  
*triserialis*, *Ophichthus* 81  
*Typhlotes* 65  
*typus*, *Achirophichthys* 65  
*unicolor*, *Ophichthus* 81  
*Uranichthys* 80,81

- urolophus*, *Ophichthus* 81  
*uropterus*, *Myrophis* 60  
*vafer*, *Myrophis* 59,60  
*velifer*, *Letharchus* 63,64  
Verma 65,66  
*vermiformis*, *Leptenchelys* 72  
*vermiformis*, *Muraenichthys* 59  
*versicolor*, *Elapsopsis* 77  
*vulturis*, *Ichthyapus* 68
- woosuitingi*, *Ophichthus* 81  
*xenodontus*, *Phyllophichthus* 82  
*xorae*, *Muraenichthys* 59  
*Xyrias* 84  
*xystrurus*, *Myrichthys* 78,79  
*Yirkala* 67,69  
*Zonophichthus* 80,81,85  
*zophistus*, *Pisodonophis* 82  
*zophochir*, *Ophichthus* 75,80,81